TEMPORAL VARIATION AND HABITAT USE OF NEARSHORE CRAB POPULATIONS IN KACHEMAK BAY, ALASKA

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A

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GENERAL ABSTRACT

Larval, juvenile, and adult crab distribution was surveyed in three different habitats in Kachemak Bay, Alaska from June 2005 to September 2006 to determine temporal and spatial variability. Crab distribution varied temporally and spatially in all life stages. Nine sites of varying habitat complexity were surveyed monthly using scuba, light traps, and shrimp pots to measure habitat variables, quantify larval, juvenile, and adult crabs, and survey potential crab predators. No single bay-wide variable determined the appearance of all crab larvae. Spatial differences in larval abundance probably resulted from large scale physical transport mechanisms. Overall juvenile and adult crab abundance increased with habitat complexity; however species richness was not positively correlated with complexity. This study suggested that the canopy structure provided by *Nereocystis luetkeana* had minimal effects on spatial crab distribution in all life stages. Canopy structure may not influence the spatial distribution of larval crabs and is thought to have little importance for juvenile and adult crabs. Understory kelp density may more directly affect juvenile and adult crabs by providing more microhabitats for refuge. Habitat use and the importance of structural complexity vary by life history stage and species depending on survival strategy.

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GENERAL INTRODUCTION

Crabs are an important trophic link in nearshore systems and have significant ecological importance. Crabs influence food web dynamics throughout their life span by acting as a food source for planktivores, fish, invertebrates, birds, and sea otters. Variations in crab densities have the potential to cause cascading effects affecting higher trophic levels. Larval crabs are a food source for planktivores. Juvenile and adult crabs also are an important food source. They are estimated to be the second most important food category for kelp-associated fish (Quast 1968, Love and Ebeling 1978). Also, one spider crab species was shown to make up approximately 25% of the prey items in sea otter diets in southern California (Hines 1982). In Alaska, approximately 70% of an intertidal octopus diet consisted of crabs (Vincent et al. 1998). Crabs also are key consumers of detritus, macroalgae, and other invertebrates (Polis and Strong 1996, Buck et al. 2003).

Crabs have a complex life cycle with pelagic and benthic forms; thus investigating temporal and spatial variation of each stage is critical for understanding crab ecology and population dynamics. A brooding female releases planktonic zoeae into the water column that are capable of transport over large distances. Depending on species, crab larvae undergo a number of zoeal stages before molting into megalopae. The megalopae settle in suitable coastal environments where they live as juveniles and adults. Temporal and spatial variation of larval crab recruitment to nearshore habitats can influence adult populations.

Biotic and abiotic factors affect crab populations. For example, recruitment and larval dynamics are thought to be influenced primarily by abiotic forces. Currents driven by wind, internal waves, tides, and upwelling events influence larval crab spatial distributions (Shanks 1995a, 1995b, Paula et at. 2001, Johnson and Shanks 2002, Miller and Shanks 2004), while temperature and salinity thresholds may influence temporal variation in larval release (Forward 1987, Morgan 1987, 1995, Shirley and Shirley 1989, Starr at al. 1990, DeVries et al. 1994, Christy and Morgan 1998, Park and Shirley 2005). Adult distributions and larval release may also be influenced by biological conditions such as predation pressure or food availability.

Habitats with three-dimensional structure such as seagrass beds, coral reefs, mangrove systems, and kelp beds add complexity to an ecosystem, which can influence crab distributions by providing many ecological niches (Hines 1982, Hixon and Beets 1993, Downes et al. 1998, Attrill et al. 2000, Ashton et al. 2003, Almany 2004, Graham 2004). The added spatial refuges in complex habitats allow many crab species to utilize concealment strategies to decrease predation and competition (Holbrook and Schmitt 1988, Lohrer et al. 2000). Food availability is higher in areas with proportionately more microhabitats and surface area that prey items can occupy (Lohrer et al. 2000).

Kelps are large brown algae in the order Laminariales and can exist in both canopy and understory forms. Kelp beds are extremely productive and diverse ecosystems that supply complex habitat to many species (Foster and Schiel 1985) and are temporally and spatially variable (Carr 1991). Interannual variability in kelp structure is a result of annual growth, senescence, nutrient limitation, sunlight, and storm events. Kelp

bed composition can also vary spatially with latitude. For example, *Macrocystis pyrifera* dominates the canopy along the Californian coast in the eastern Pacific, while at higher latitudes, *Nereocystis luetkeana* and *Alaria fistulosa* characterize the canopy species. *Macrocystis pyrifera* differs in physical structure from these kelps as it has dense mid-water blades. *Alaria fistulosa* forms a long, narrow blade that extends to the surface, while *N. luetkeana* has a long rope-like stipe extending to several blades at the surface of the water. Because *A. fistulosa* and *N. luetkeana* often do not grow in high densities, an abundant understory can thrive, resulting in a highly complex three-dimensional habitat. Kelp understory exists in varying densities depending on local conditions, consisting of both annual and perennial species. These species are structurally similar in size and shape. Kelp structure can alter small scale localized hydrodynamics (Eckman et al. 1989, 2003), which may influence larval crab assemblages in these areas. Understory kelp structure also can act as refuge for juvenile and adult crabs by increasing availability of microhabitats (Hines 1982).

This study documents temporal and spatial distributions of crabs in all life history stages in south-central Alaska. It also attempts to understand the role of biogenic structure provided by kelp beds in the spatial distribution of larval, juvenile, and adult crabs. Nine nearshore sites in Kachemak Bay, Alaska were surveyed over 16 months for habitat variables and larval, juvenile, and adult crab distribution and abundance. The sites varied in kelp density and bottom topography. Three sites had a kelp canopy and understory community, three sites only contained a kelp understory community, and the remaining three sites were sand.

Chapter 1 focuses on temporal variation of larval crabs and potential effects of kelp structure on spatial variation. Temporal and spatial variability among species was most likely due to species specific tolerances to several environmental variables and large scale physical transport mechanisms. No single bay-wide trend determining the appearance of all species was apparent.

Chapter 2 focuses on temporal and spatial distribution of juvenile and adult crabs in kelp habitats with varying levels of complexity and explores the possibility of predator interactions influencing crab distribution. Kelp structure did not have equal importance for all species and varied with species survival strategy. The synergistic relationship of habitat complexity and predation is a fundamental concept influencing habitat use and distribution of nearshore crabs.

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CHAPTER 1:

Temporal And Spatial Variability Of Nearshore Crab Larvae In Different Habitats Within Kachemak Bay, Alaska[1]

ABSTRACT

Larval crab distribution was surveyed in three different habitats in Kachemak Bay, Alaska to determine temporal and spatial variability. Distribution varied temporally and spatially from June 2005 to September 2006. Nine sites of varying habitat complexity were surveyed monthly using scuba and light traps to measure habitat variables and quantify larval crabs. A total of 10,016 larval crabs belonging to seven families were identified. Four species comprised the majority (97%) of the total larval assemblages and included *Cancer oregonensis, Fabia subquadrata, Telmessus cheiragonus,* and *Pugettia gracilis*. Peak abundances occurred in summer but varied on small temporal scales (days and weeks) with species. No single bay-wide variable determined the appearance of all species. Depending on species, appearance may be influenced by seasonality of environmental variables. Spatially, highest abundances occurred in habitats with less structural complexity. Spatial differences in larval abundance may have resulted from large scale physical transport mechanisms. For example, the canopy kelp density may not have been sufficient to alter small scale hydrodynamics affecting larval assemblage distribution.

[1] Daly B, Konar B (2007) Temporal and spatial variability of nearshore crab larvae in different habitats within a high-latitude region. Prepared for submission in Marine Ecology Progress Series

INTRODUCTION

Larval crab distribution is variable in time and space. Though extensive literature exists on larval biology of crabs, much of the research focuses on commercially important species (Lipcius et al. 1995, Lochmann et al. 1995, Loher and Armstrong 2001, Johnson and Shanks 2002, Stevens 2003, deRivera et al. 2005, Pedersen et al. 2006), which can be instructive for non-commercial species. However, species specific behavior can interact with hydrodynamic processes making temporal and spatial variation difficult to generalize (Shanks 1995a, see Queiroga and Blanton 2005 for review). Non-commercial species may be important trophic links or have significant ecological importance as key consumers and a food source for other organisms (Hines 1982, Polis and Strong 1996). Thus, the timing and seasonality of larval crab recruitment to nearshore habitats may be important in shaping the spatial distribution of adult populations (Quijon and Snelgrove 2005). Documenting larval crab distribution in time and space is valuable in determining the natal origin of cohorts and may be a critical step in understanding dispersal patterns and population connectivity.

Some crab species use broadcast strategies to maximize their reproductive efficiency. A brooding female may release thousands to millions of planktonic zoeae into the water column. Depending on species, crab larvae undergo a number of zoeal stages before molting into megalopae. Species with lengthy planktonic larval periods are capable of transport over large distances and may recruit into spatially separate communities (Queiroga and Blanton 2005, Park et al. 2007). Some larval species remain nearshore, while others are carried offshore until they return as megalopae to settle in

suitable coastal environments (Lough 1974, Paula et al. 2001, Mace and Morgan 2006) where they live as juveniles and adults. Because most crab larvae are unable to swim against horizontal currents because of high energetic costs or physical limitations, the return to nearshore habitats is likely aided by shoreward currents (Paula et al. 2001; Johnson and Shanks 2002). Transport mechanisms such as tides, internal waves, wind patterns, upwelling events, and density-driven currents are thought to transport invertebrate larvae (Shanks 1995a, 1995b, Paula et al. 2001, Johnson and Shanks 2002, Miller and Shanks 2004, see Queiroga and Blanton 2005 for review). The effects of large scale biotic variables such as biogenic structure, predation, food availability, and behavior on temporal and spatial variation of nearshore larval abundance are relatively less understood (see Roughgarden et al. 1988, Wolanski and Hamner 1988, Duggins et al. 1990).

The timing of larval release by crabs may be triggered by multiple environmental cues including tides, temperature, salinity, light, phytoplankton blooms, and predation (Forward 1987, Morgan 1987, 1995, Shirley and Shirley 1989, Starr et al. 1990, DeVries et al. 1994, Christy and Morgan 1998, Park and Shirley 2005, Fisher 2006). These physical and biological variables are strongly correlated with season and temporal variability of larval dispersal. The appearance of many brachyuran species coincides with oceanic conditions that are favorable to their survival (high food availability, light, temperature) (Fisher 2006). However, seasonal timing on small temporal scales (days or weeks) within favorable environmental conditions is less understood. Larval timing may

vary by species more in high latitudes as a way of optimizing specific environmental conditions (Park and Shirley 2005).

The spatial distribution of invertebrate larvae may depend on an interaction between physical processes (hydrodynamics) and small scale events (behavior) (Jackson 1986, Duggins et al. 1990, Mace and Morgan 2006). Larval crabs may regulate their vertical position to enhance or minimize hydrographic processes (see Queiroga and Blanton 2005 for review). Blue crab larvae settle to the benthos during low flow regimes and vertically rise during high flow regimes, which are associated with changing tidal cycles resulting in a net migration in a specific direction (Sandifer 1975, Tankersley and Forward 1994, Lochman et al. 1995). Diel vertical migration enables crab larvae of certain species to control their distribution using tidal stream transport and various flow fields (Little and Epifanio 1991, DeVries et al. 1994).

Biogenic structure may affect hydrodynamic processes influencing the spatial orientation and distribution of crab larvae. Mid-water structure provided by kelps can alter flow regimes and hydrodynamics on small spatial scales (Eckman et al. 1989, 2003). Understory kelps (plants with short stipes and blades extending no more than a few meters above the benthos) inhibit water flow and particle transport causing higher rates of particle deposition in these habitats (Eckman et al. 1989). Higher deposition may be the result of longer residence times and not higher rates of import (Eckman et al. 1989, Duggins et al. 1990). Canopy kelp (plants with long stipes and blades that extend to the surface of the water) affect small-scale current regimes (Jackson and Winant 1983). The canopy kelp *Macrocystis pyrifera* provides much mid-water structure and has been used

in most studies involving hydrodynamics in kelp beds (Duggins et al.1990). *Macrocystis pyrifera* beds slow nearby currents to roughly 33% of their original velocity (Jackson and Winant 1983). The transition of flow near the up-current edge of these canopy kelp beds has the strongest gradient causing an equilibrium state within the beds. This edge effect may limit the penetration of planktonic larvae into dense canopy stands (Jackson and Winant 1983, Jackson 1984, 1986, Duggins et al. 1990). Kelp beds also dampen high frequency variance and slow low frequency wave propagation of internal waves (Jackson 1984). Because crab larvae may be pelagic for months and rely on physical transport mechanisms, local changes in hydrodynamic processes could alter their local assemblages.

Nereocystis luetkeana is the predominant canopy kelp in south-central Alaska. It provides structure on the surface of the water, where blades can grow to 11 m. Although adults provide little mid-water structure, juvenile *N. luetkeana* found in beds are typically of various heights, which results in mid-water structure throughout the water column (Daly, personal observation). The multi-bladed structure of *N. luetkeana* can alter flow regimes (Koehl and Wainwright 1977, Hurd and Stevens 1997), which could possibly lead to localized alterations in larval crab assemblages. *Nereocystis luetkeana* beds associate with complex rocky substrate and relatively high levels of ambient current. Hydrodynamic effects on benthic invertebrate recruitment are rarely studied in topographically complex habitats with high ambient current velocities (Duggins et al. 1990).

In Alaska, seasonality and the potential effects of habitat on spatial distribution are poorly understood for most crabs. Field studies of larval dynamics can be logistically difficult in remote high latitude regions with short field seasons where weather and sea conditions can be adverse. This study, which surveyed all nearshore larval crabs in a high latitude region, had two facets: (1) to compare temporal variability among species in the zoeal and megalopal stages; and (2) to compare habitat use among species over time regardless of larval stage. I hypothesized that (1) temporal variability of zoea and megalopae is similar among predominant crab species; and (2) larval abundance of the predominant species has temporal variability among habitat types.

MATERIALS AND METHODS

Study area. This study was conducted in Kachemak Bay, located in lower Cook Inlet, Alaska (Fig. 1.1, 59°30'N, 151°30'W). This estuarine bay has a large tidal range with fluctuations of up to 10 m. The southern part of the bay is strongly influenced by oceanic input from the Gulf of Alaska. Surface and deep-water currents are counter clockwise, moving water from the Gulf of Alaska into Kachemak Bay along the southern shore and exit along the northern shore (Baird and Pegau 2006).

Nine sites were selected in Kachemak Bay based on structural habitat characteristics including substrate size and rugosity, which were measured during site selection in May 2005. Three sites had a kelp canopy and understory community, three sites only contained a kelp understory community, and the remaining three sites were sand. All sites were separated by at least 1 km and were the same approximate size (approximately 2800 m^2) and depth (approximately 10 m) to eliminate these factors as

covariates. Sites were surveyed (see below) monthly for 16 months beginning in June 2005. Physical characteristics (temperature, salinity) were measured in September 2006.

Habitat surveys. Kelp densities were measured monthly from June 2005 to September 2006 to document seasonal variation. The only canopy kelp was *Nereocystis luetkeana*, while understory kelps included *Laminaria* spp., *Saccharina* spp., *Agarum clathratum*, *Costaria costata*, and *Cymathaere triplicate*. To quantify understory kelps at each site, individuals were identified and counted in six randomly placed 0.25 m^2 quadrats along three 30 m transects. Because all understory kelp species are structurally similar in Kachemak Bay (in size and overall shape), they were grouped as understory for statistical analyses. Since canopy kelp are rare compared to understory species, all canopy individuals within each 30 m^2 transect were enumerated. Juvenile canopy kelp can be the same height as understory kelp so only individuals contributing to the canopy (approximately 2 m above understory) were counted as canopy kelp. Smaller canopy juveniles (<2 m) were considered understory.

Average substrate size and rugosity were measured along nine 30 m transects at each site in May 2005 and September 2006 to quantify habitat complexity. Substrate size was determined by measuring the diameter of the dominant substrate type at six random points along each transect. Rugosity is defined as the contour distance along the bottom per meter of horizontal distance and was measured using a one-meter-long polyvinylchloride (PVC) bar with several 5 mm chain links attached to one end (Hamilton and Konar 2007). At six random points along each transect, the bar was placed horizontally so that the chain links draped over the substrate. The chain was then

measured per meter of horizontal distance. Rugosity and substrate size values for each site were averaged to determine values for each site. Sites were selected so kelp containing sites had similar substrate complexity. Substrate rugosity in sand was assumed to be one.

Larval crab surveys. Light traps were used to collect larval crabs at each site. Each trap was constructed of a 19-L, translucent water jug with side openings for planktonic organisms to enter and a PVC pipe with 330 μm mesh on the bottom. Two battery powered LED dive flashlights (PrincetonTec, Attitude®) inside the jug attracted larval organisms (Reyns and Sponaugle 1999, Roegner et al. 2003, Miller and Shanks 2004, Herter 2007). Planktonic organisms that enter the trap cannot easily exit because openings are funnel-shaped and point inward. Traps were attached to a mooring line 6 m above the seafloor. Traps emit light for only a few meters so each trap was separated by at least 5 m to ensure independent replicates. Traps were retrieved via the mooring line, plankton were collected on mesh at the bottom of the trap, and samples were preserved for later analysis. Larval crabs were counted and identified to the lowest possible taxonomic level (Hart 1935, 1960, Lough 1974, Adams 1979, Haynes 1981, DeBrosse et al. 1989, Ko 1998, Shanks 2001, McLaughlin et al. 2005). Three traps were deployed monthly for two days at each site for 16 months during neap tide. In summer (June until mid September 2005) traps were deployed weekly.

Statistical analysis. Statistical analyses were performed using linear models and multivariate approaches with STATISTICA v.6 and PRIMER v.6 (Statsoft, Tulsa, OK, USA). Multidimensional scaling (MDS) analysis (Field et al. 1982) was used to examine

habitat variability among sites. Data were ranked and Euclidian distance calculated (Trainor and Church 2003). Repeated measures analysis of variance (ANOVA) was used to determine significance in kelp density among habitats over time, while one-way ANOVA tested for differences in substrate complexity, temperature, and salinity. Repeated measures ANOVA was used to test for significance in overall larval abundance and dominant species among habitats over time. Post-hoc comparisons (Tukey's Honestly Significant Difference) were also used to determine significance in temporal variation of larval crab abundance and habitat variables among habitats. Values for kelp and larval abundance are listed as mean ± one standard error. Units for kelp density are listed as stipes per area and larval abundance is listed as larvae per trap. Significance was determined with an alpha level of 0.05.

RESULTS

Habitat. Sites were grouped by habitat similarity using four variables: substrate rugosity, substrate size, understory kelp density, and canopy kelp density (Multi-dimensional scaling (MDS) analysis, Fig. 1.2). All kelp sites grouped separately from sand sites indicating that substrate complexity was dissimilar between kelp and sand sites. Within all kelp sites, the three canopy sites grouped separately from the understory sites suggesting heterogeneity in kelp communities (Fig. 1.2, MDS analysis).

All kelp sites had a strong seasonality with highest kelp densities in summer decreasing through winter (Fig. 1.3). Significantly higher canopy densities occurred in summer 2006 than 2005 (Tukey's HSD, $p < 0.0001$), while understory density was comparable between summers. Canopy density was significantly different among habitats

(Table 1.1) with canopy sites having significantly more canopy than sand (Tukey's HSD, $p < 0.0001$) and understory (Tukey's HSD, $p < 0.0001$) sites. Canopy sites had a mean canopy density of 5.29 ± 0.71 stipes $\cdot$ 60 m^{-2}, while understory sites had a mean canopy density of 0.31 ± 0.12 stipes $\cdot$ 60 m^{-2}. No canopy was found at sand sites. Also, canopy density at the canopy sites had a strong interaction with seasonality (Tukey's HSD, $p < 0.0001$) as *Nereocystis luetkeana* is an annual species.

Understory density was significantly different among habitats (Table 1.1) with all habitats being significantly different from each other. Canopy sites had the highest overall understory mean density of 4.45 ± 0.017 stipes $\cdot$ 0.25 m^{-2}, followed by understory sites with a mean density of 3.04 ± 0.122 stipes $\cdot$ 0.25 m^{-2}. Sand sites had very little understory (0.08 ± 0.142 stipes $\cdot$ 0.25 m^{-2}). Understory kelps also had a strong interaction with season with more density fluctuations at the canopy sites (Fig. 1.3A).

Substrate rugosity was significantly different among habitats (Table 1.1) with kelp sites being similar but significantly different than sand sites (Tukey's HSD, $p < 0.0001$). No significant changes in substrate complexity occurred over time (ANOVA $p = 0.292$). No significant differences in temperature (ANOVA, $p = 0.965$) and salinity (ANOVA, $p = 0.690$) were found among sites.

Crab larvae. A total of 10,016 larval crabs belonging to seven families were caught in the light traps. Most larvae were identified to species, although some (Table 1.2) were assigned to higher taxonomic levels. The most abundant species included *Cancer oregonensis, Fabia subquadrata, Telmessus cheiragonus,* and *Pugettia gracilis*; these four species comprised the majority (97%) of the total larval assemblages (Table

1.2). Several majid individuals were unidentifiable and were grouped as Majidae. All lithodid crabs were grouped as such and pagurids were excluded. Some individuals were unidentifiable due to poor preservation and were classified as unknown.

Larval assemblages were strongly seasonal with peak abundances in late summer. In general, megalopae had a maximum slightly later than zoeae with very few larvae caught in winter. Strong seasonality occurred in overall larval abundances with no significant differences in habitat variability (Repeated measures ANOVA, Table 1.3). However, temporal variability was significantly different between sand and canopy sites (Tukey's HSD, $p = 0.0419$). Differences in larval abundances between sand and understory or understory and canopy sites were not significant.

The predominant species varied over time in both larval stages and overall abundances (Fig. 1.4, 1.5). *Cancer oregonensis* was the most abundant species (60% of total larvae observed) with maximum zoeae during mid summer (July) followed by highest megalopae abundances shortly thereafter. *Fabia subquadrata* was second in abundance (31.7% of total larvae observed) with maximum zoeae in late July in both 2005 and 2006, followed by very small numbers of megalopae. *Telmessus cheiragonus* (3.5% of total larvae observed) had large isolated numbers of zoeae in April and megalopae in August through September. *Pugettia gracilis* (2% of total larvae observed) had highly pulsed numbers of zoeae and megalopae appearing throughout the summer with highest abundance in late July and early August. All of the most abundant species varied over time (Repeated measures ANOVA, $p < 0.0001$) (Table 1.3).

The predominant species also varied in habitat use (Fig. 1.6, 1.7). Habitat use was not significant for most species. *Telmessus cheiragonus* was the only species in which abundance varied significantly between habitats (Table 1.3). Pooled across habitat types, the abundance of all predominant species differed significantly over time, with most species occurring in summer. Significant habitat by time interaction did not occur for any of the most abundant species.

DISCUSSION

Environmental variables including tides, temperature, salinity, light, phytoplankton blooms, and predation are seasonally pulsed and may serve as cues for larval release (Morgan 1987, Shirley and Shirley 1989, Starr et al. 1990, Morgan 1995, Park and Shirley 2005, Fisher 2006). Larval crab seasonality may vary more in high latitudes where environmental forces are more dramatic (Park and Shirley 2005). Kachemak Bay, where this study occurred, is at a relatively high latitude (59° 30′ N) and has extreme daily tidal fluctuations (up to approximately 10 m) and severe seasonal variations in temperature, salinity, and light/dark regimes. This study demonstrated that at this high latitude site, larval crab release times and spatial distribution are highly variable with species.

Temporal variations in timing may have evolved to reduce physiological stress resulting from unfavorable conditions (Christy 1982, Morgan 1987). In general, low temperature causes lower metabolic rates, which slows development. A slower development results in longer exposure to predation by pelagic organisms, which may increase mortality. In this study, *Telmessus cheiragonus* and *Pugettia gracilis* larvae

appeared in the water column earliest in the year compared to other species, with high numbers of zoeae occurring in mid-April, when water temperature was approximately 5°C. In Japan, *Telmessus* spp. first appears in the middle of March (Ueda et al. 1999), while *Pugettia* spp. appear when a minimum temperature of 13°C is reached (Kornieko and Korn 2004). Water temperature in Kachemak Bay reaches a maximum of 13°C in late summer, much later than when *P. gracilis* first appeared. Interestingly, *P. gracilis* and *T. cheiragonus* have similar ranges, occurring from Alaska to Monterey, California (Jensen 1995). Thus far, *Telmessus* spp. and *Pugettia* spp. have been largely studied at lower latitudes (Ueda et al. 1999, Kornieko and Korn 2004), where temperatures are warmer. This study suggests that *Telmessus* spp. and *Pugettia* spp. larvae can tolerate low temperatures, which may give a competitive advantage in high latitudes where windows of favorable conditions are narrow. In comparison to *Telmessus* spp. and *Pugettia* spp., *Cancer oregonensis* and *Fabia subquadrata* were first observed in late June 2005 and 2006 and occur from Alaska to southern California (Jensen 1995). These two latter species may require higher temperatures to develop most efficiently. Larval *C. oregonensis* were also observed in June in southeastern Alaska (Park and Shirley 2005), and in Puget Sound had optimum development at 10-15°C temperatures (Sulkin and McKeen 1994). These temperatures are similar to those recorded in mid to late summer in Kachemak Bay. Little is known about physical tolerances of *F. subquadrata.*

Dietary demands may be species specific and require a certain prey composition to develop optimally. Zoeae are omnivorous (Welch and Epifanio 1995) and have specific nutritional requirements that are satisfied by particular prey assemblages (Paul et

al. 1989, Sulkin et al. 1998). Phytoplankton may provide ancillary nutrition when ingested in combination with certain zooplankton (Sulkin and Epifanio 1975). Prey items vary in their degrees of nutritional value. Crab larvae require certain amounts of long-chain polyunsaturated fatty acids, which are unique in plankton groups (Welch and Epifanio 1995). Because crab larvae use encounter feeding strategies, prey density and composition may play critical roles in determining larval release. Depending on the plankton assemblage present, brooding females may release their zoeae to coincide with the appearance of specific species. In this study, compared to other species, *Pugettia gracilis* and *Telmessus cheiragonus* appeared in the water column earliest in the year. Prey appearing solely in the early larval stages was shown to be sufficient to support development in *F. subquadrata* (Harris and Sulkin 2005). As such, synchronizing eclosion of *F. subquadrata* with plankton blooms could be less critical. A delayed release during a bloom may allow larvae to feed and remain in the water as phytoplankton levels drop.

In this study, spatial variability in larval abundance occurred for all crab species. Overall, sand sites had significantly higher larval abundances than canopy sites. Field studies have demonstrated that kelp habitats can significantly affect localized hydrodynamics (Jackson and Winant 1983, Jackson 1984, 1986, Eckman et al. 1989, Duggins et al. 1990, Eckman et al. 2003). Added canopy structure may produce a strong flow gradient at kelp bed edges, reducing penetration. However, because there was no significant difference in larval abundance between understory and canopy sites, canopy structure was probably not the principle agent behind these differences. Canopy densities

in *Nereocystis luetkeana* beds may be too low to affect the hydrodynamics influencing larval distributions. Understory provides no structure in the mid-water, and has little effect on planktonic organisms near the canopy. Differences in spatial distributions are most likely determined by large scale physical transport mechanisms. By species, only *Telmessus cheiragonus* had significant differences in abundance in different habitats, with highest numbers at sand sites. Although not significant, *Pugettia gracilis* had a higher proportion of larvae at canopy sites than other predominant species. Most *P. gracilis* larvae were megalopae, suggesting individuals may aggregate in these habitats to settle. Adult densities of *T. cheiragonus* and *P. gracilis* were also highest in these respective habitats (Daly and Konar 2007). Adult populations are thought to have little effect on larval assemblages on the small spatial scales in this study. High ambient current velocities would cause zoeae to be quickly transported away from release sites.

Sampling bias may have influenced light trap efficiency. Traps might be expected to sample more effectively in winter as ambient light levels are lower due to shorter daylight hours. However, overall organism abundance was lower in winter suggesting that seasonal differences in abundance are most likely due to life history traits. Between habitats, trap effectiveness may explain differences in abundance. Trap visibility, the added trap structure and differences in predation may have affected catch efficiency. The increased structure of *Nereocystis luetkeana* could obstruct the traps from larval view. Because sand sites had no kelp, traps may have been more visible to larvae. Also, larvae may be less likely to leave the canopy structure to enter traps. In sandy areas with no mid-water structure, larvae may be more attracted to the added trap structure. Increased

predation could be determining lower larval abundances in kelp habitats, as fish abundance was higher in kelp habitats (Daly, personal observations).

This study supports the importance of documenting temporal and spatial variability and habitat structure. Other high latitude locations may have similar trends in larval dynamics. The dramatic seasonality of environmental variables may regulate the timing of larval hatching. Temporal variability among species was most likely due to species specific tolerances to several physical and biological variables. No single bay-wide trend determining the appearance of all species was apparent. Spatial distribution was variable between species. The general trend was that highest larval abundances occurred in habitats with the least structural complexity. Spatial differences in larval abundance probably resulted from large scale physical transport mechanisms. The canopy density observed probably was insufficient to alter small scale hydrodynamics enough to affect local larval assemblages. Larval crab appearance was species specific and varied on small temporal and spatial scales.

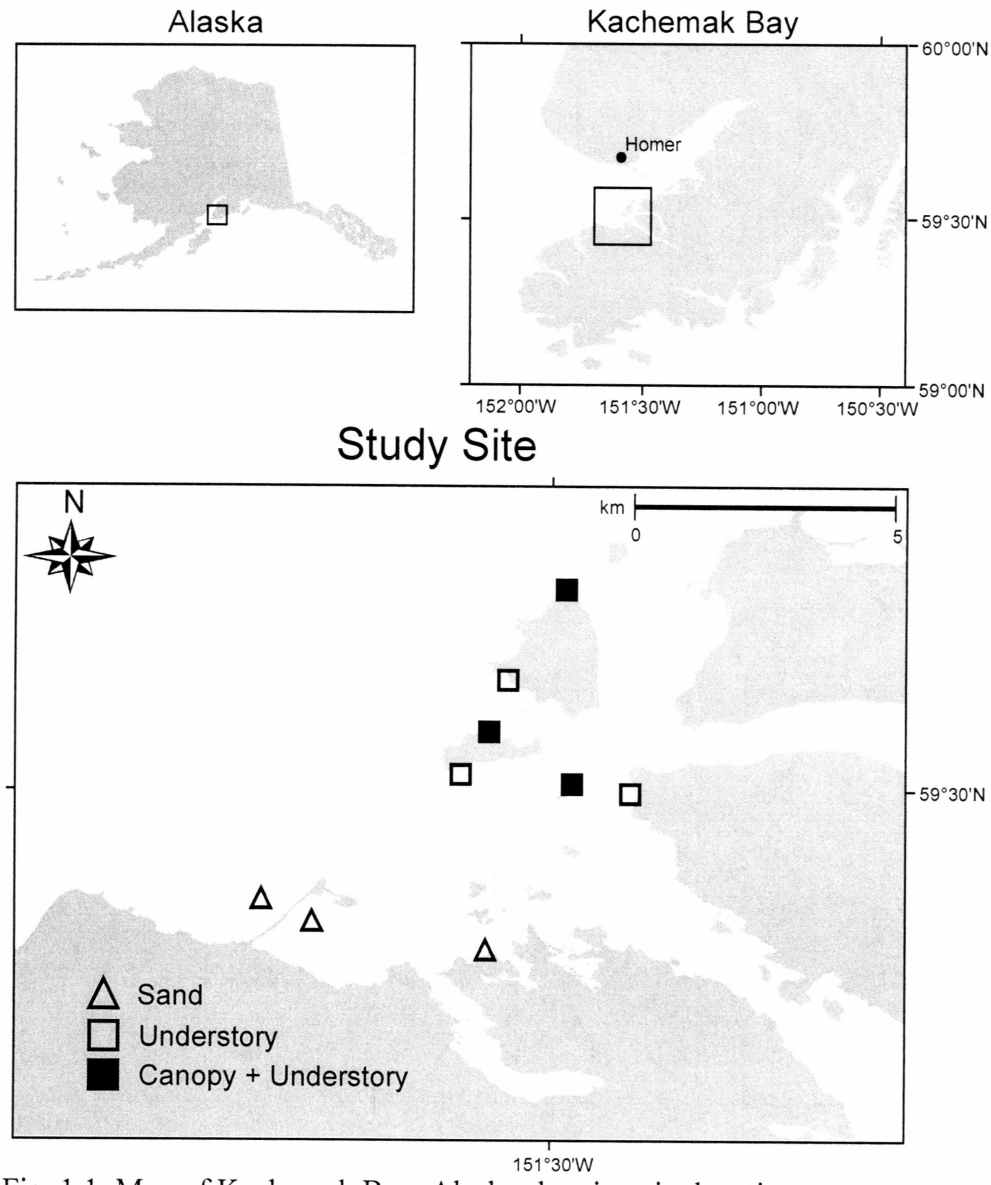

Fig. 1.1. Map of Kachemak Bay, Alaska showing site locations.

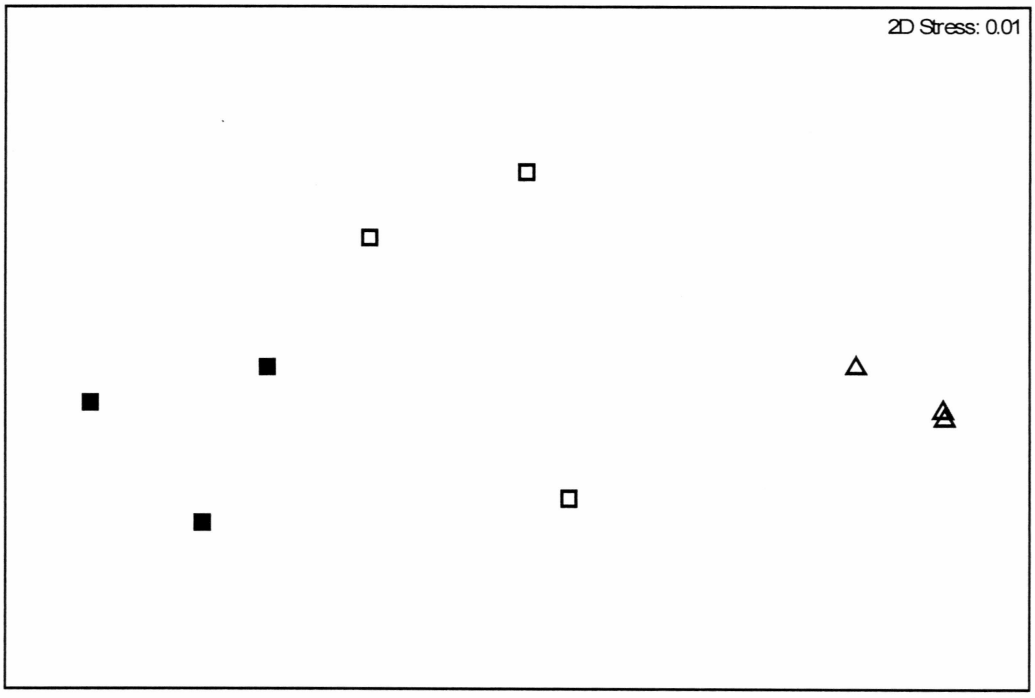

Fig. 1.2. Multi-dimensional scaling (MDS) plots of sites calculated from Euclidean distance on ranked canopy density, understory density, substrate rugosity, and substrate size variables: (sand △, understory □, canopy ■).

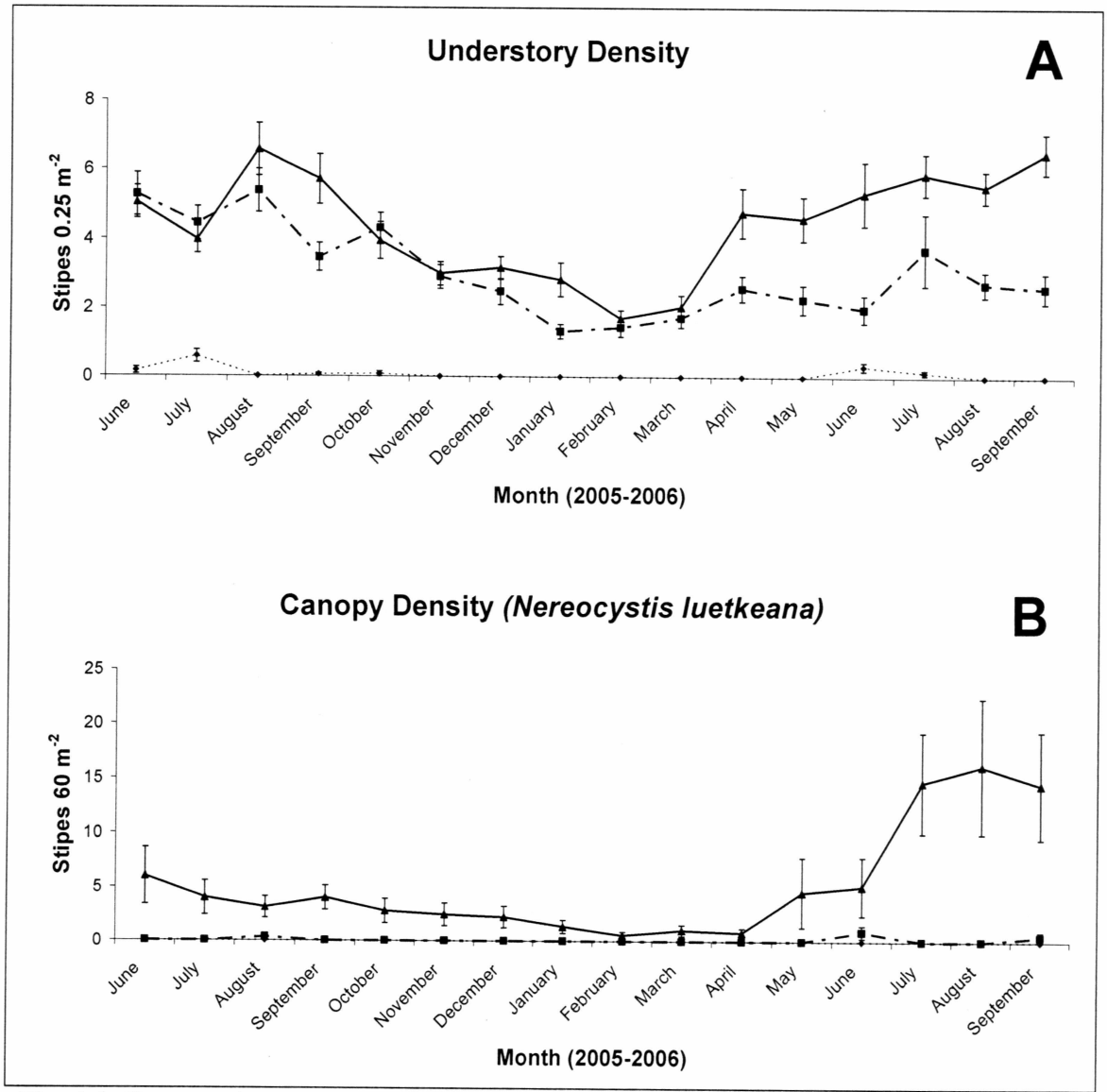

Fig. 1.3. Temporal variation of kelp density. (A) Average understory density (stipes $0.025m^{-2}$). (B) Average *Nereocystis luetkeana* canopy density (stipes 60 m^{-2}). Solid lines indicate canopy and understory habitat, dashed lines indicate understory only habitat, dotted lines indicate sand habitat. Error bars are ± 1 standard error.

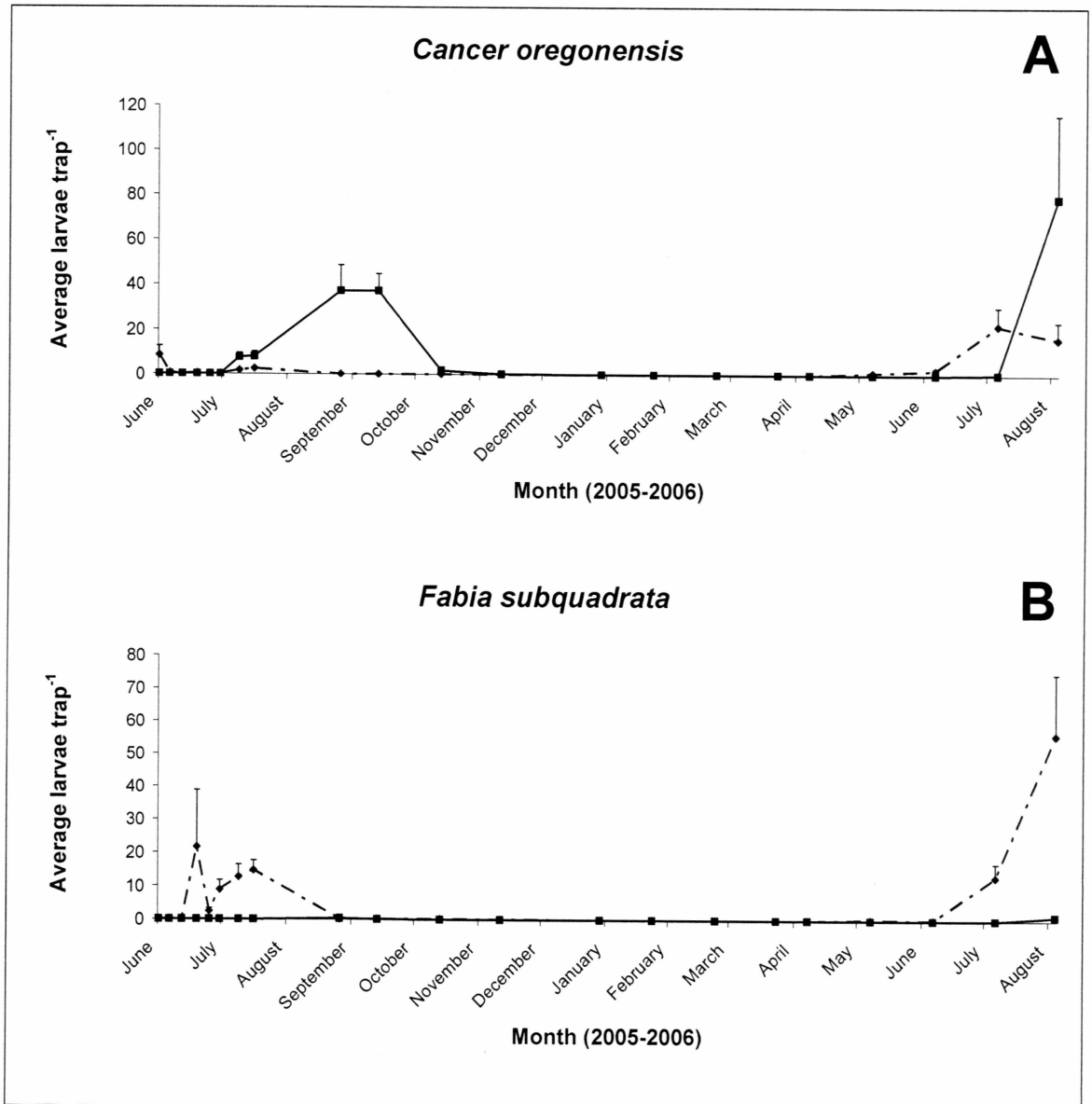

Fig. 1.4. *Cancer oregonensis* (A) and *Fabia subquadrata* (B). Temporal variation in larval abundances (larvae trap^{-1}). Solid lines indicate megalopae, dashed lines indicate zoeae. Error bars are + 1 standard error.

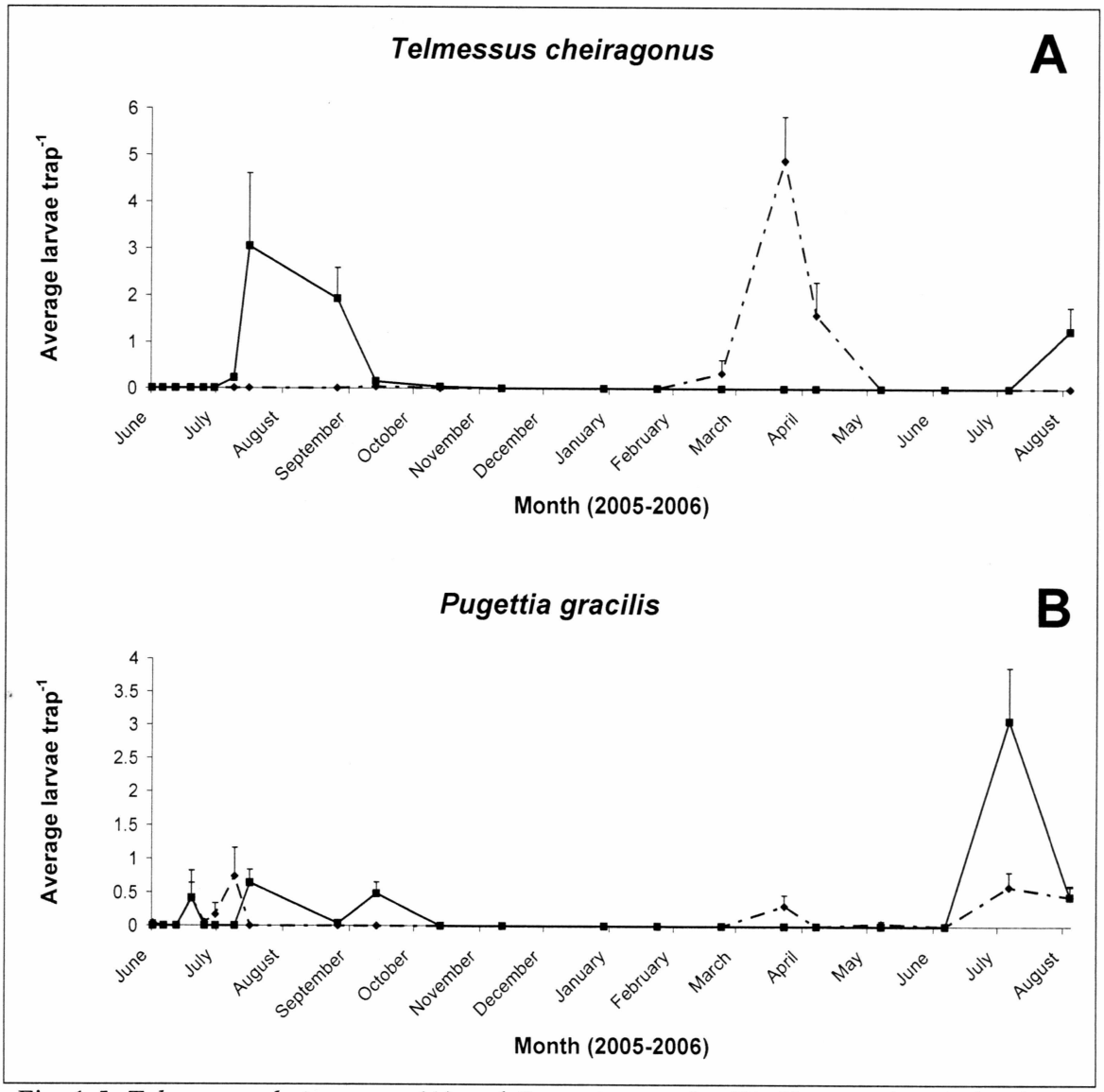

Fig. 1.5. *Telmessus cheiragonus* (A) and *Pugettia gracilis* (B). Temporal variation in larval abundances (larvae trap^{-1}). Solid lines indicate megalopae, dashed lines indicate zoeae. Error bars are + 1 standard error.

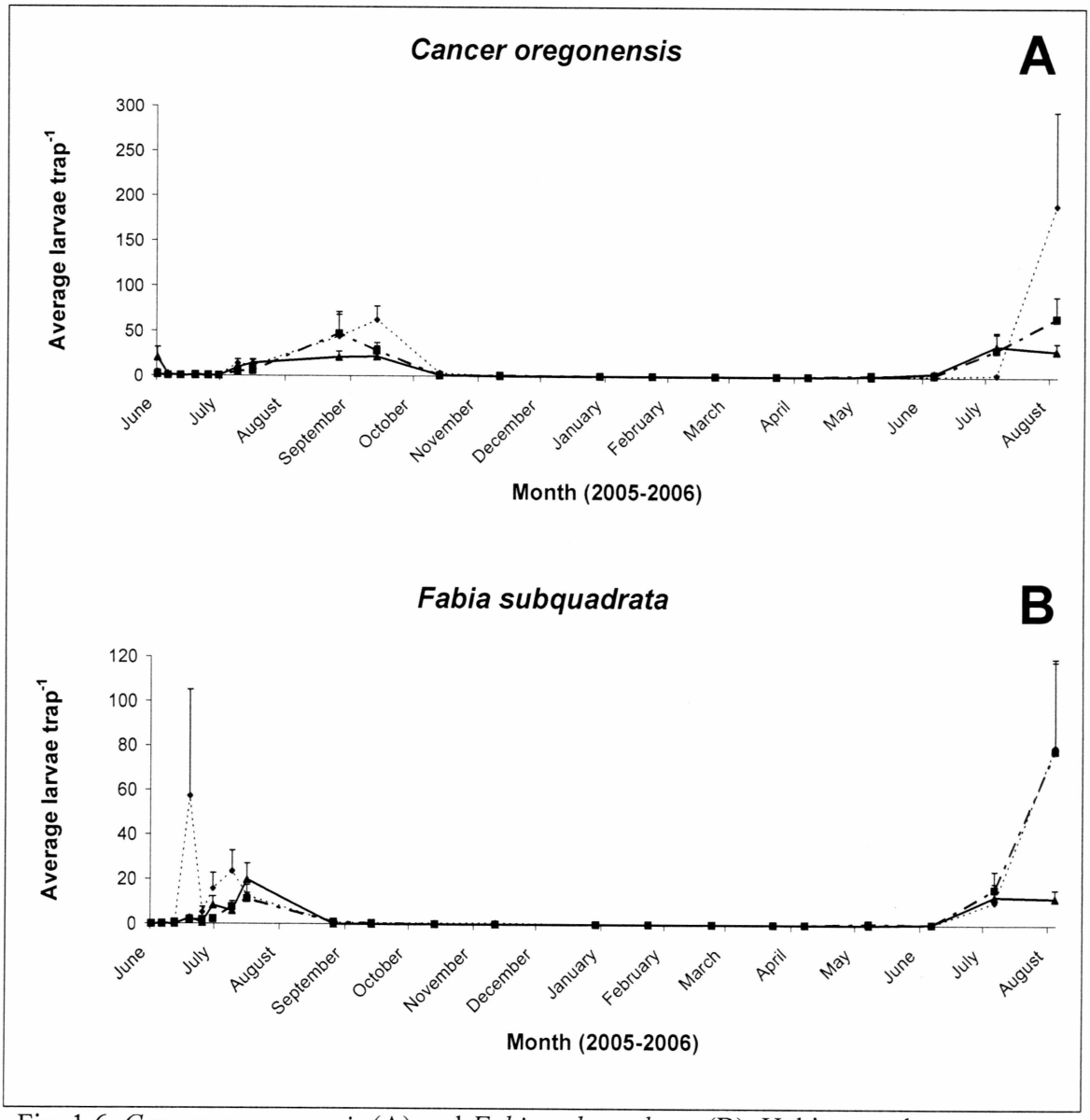

Fig. 1.6. *Cancer oregonensis* (A) and *Fabia subquadrata* (B). Habitat use by predominant species; all larval stages combined (larvae trap^{-1}). Solid lines indicate canopy and understory habitat, dashed lines indicate understory only habitat, dotted lines indicate sand habitat. Error bars are + 1 standard error.

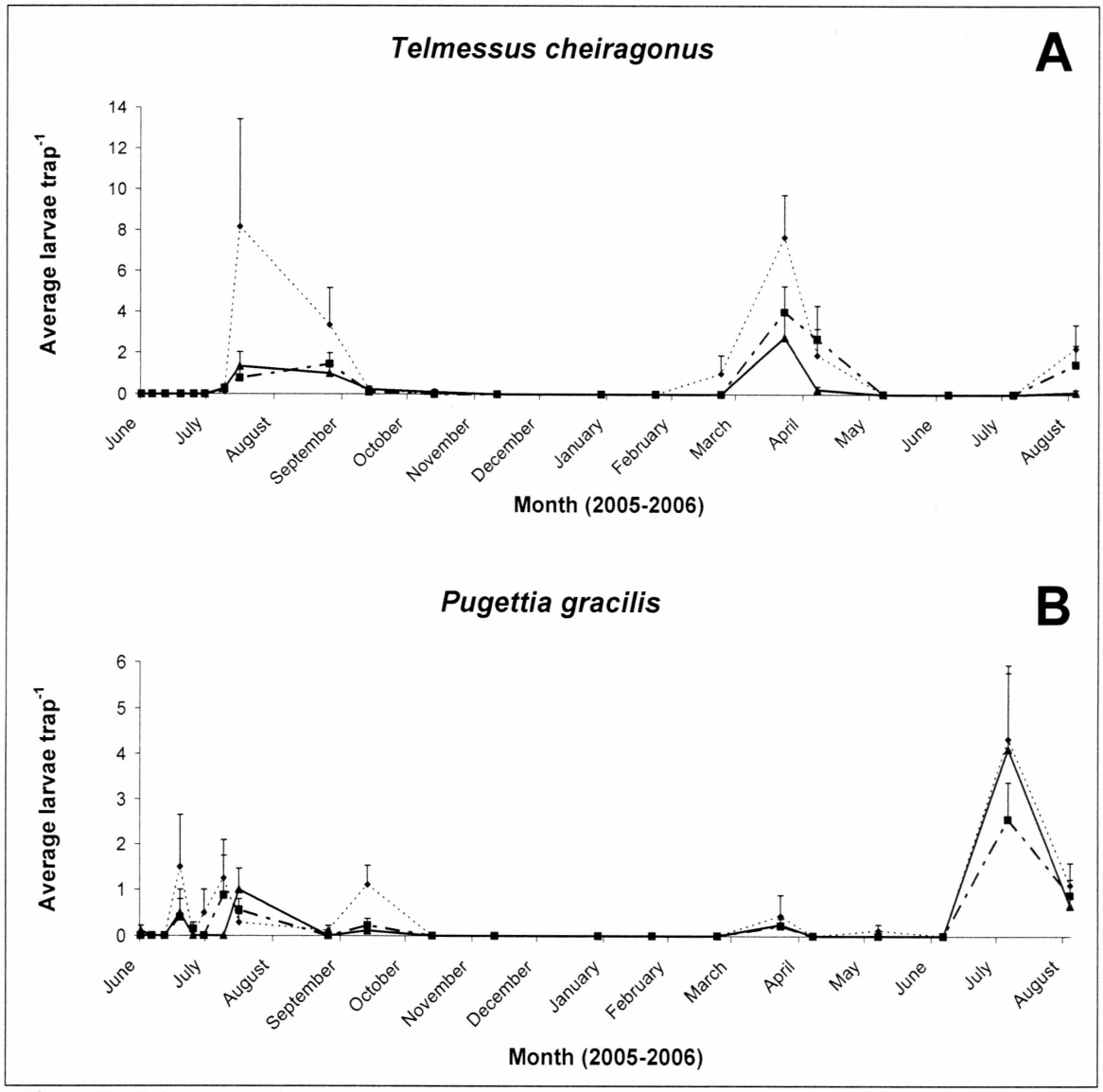

Fig. 1.7. *Telmessus cheiragonus* (A) and *Pugettia gracilis* (B). Habitat use by predominant species; all larval stages combined (larvae trap^{-1}). Solid lines indicate canopy and understory habitat, dashed lines indicate understory only habitat, dotted lines indicate sand habitat. Error bars are + 1 standard error.

Table 1.1. ANOVA statistics for habitat variables. Repeated measures ANOVA was used for kelp density to test for effects of time, habitat variability, and a habitat time interaction. One-way ANOVA was used for substrate rugosity. Bold indicates statistical significance (α less than or = 0.05).

Habitat Variable	Source	SS	df	MS	F	p
Canopy density	Date	1255.55	15	83.70	3.184	**0.0002**
	Habitat	2531.95	2	1265.98	51.875	**< 0.0001**
	Habitat x Date	2396.50	30	79.88	3.273	**< 0.0001**
	Error	6247.56	256	24.41		
Understory density	Date	1639.93	15	109.33	11.622	**< 0.0001**
	Habitat	8394.42	2	4197.21	410.825	**< 0.0001**
	Habitat x Date	1513.24	30	50.44	4.937	**< 0.0001**
	Error	16959.43	1660	10.22		
Substrate rugosity	Habitat	11.10	2	5.55	126.524	**< 0.0001**
	Error	19.83	452	0.04		

Table 1.2. Crab species caught with light traps during the 16 month study. Bold indicates the predominant species.

	Larval stage		Total
Family, *species name*, common name	zoeae	megalopae	
Cancridae			
Cancer oregonensis (pygmy rock crab)	1476	4545	**6021**
Cancer magister (Dungeness crab)	7	26	33
Pinnotheridae			
Fabia subquadrata (mussel crab)	3135	43	**3178**
Cheiragonidae			
Telmessus cheiragonus (helmet crab)	180	172	**352**
Majidae			
Pugettia gracilis (graceful kelp crab)	66	132	**198**
Chionoecetes bairdi (Tanner crab)	2	6	8
Oregonia gracilis (graceful decorator crab)	24	4	28
Unknown majid	43	0	43
Lithodidae			
Unknown lithodid	60	0	60
Xanthidae			
Lophopanopeus bellus (black-clawed crab)	11	41	52
Unknown			
Unknown	11	22	33
Grapsidae			
Hemigrapsus spp. (shore crab)	8	2	10
Total	**5023**	**4993**	**10016**

Table 1.3. Repeated measures ANOVA results for predominant species. Repeated measures ANOVA was used for predominant species to test for effects of time, habitat variability, and a habitat time interaction. Bold indicates statistical significance (α less than or = 0.05).

species	**Source**	**SS**	**df**	**MS**	**F**	**p**
C. oregonensis	Date	261422.8	20	13071.14	6.172	**< 0.0001**
	Habitat	5399.2	2	2699.58	0.998	0.3702
	Habitat x Date	140341.1	40	3508.53	1.296	0.1198
	Error	736126.0	272	2706.35		
F. subquadrata	Date	85773.7	20	4288.69	9.572	**< 0.0001**
	Habitat	1306.3	2	653.15	0.926	0.3972
	Habitat x Date	27774.9	40	694.37	0.985	0.5016
	Error	191774.3	272	705.05		
T. chieragonus	Date	780.6	20	39.03	6.671	**< 0.0001**
	Habitat	57.0	2	28.48	4.608	**0.0108**
	Habitat x Date	338.6	40	8.46	1.369	0.0778
	Error	1681.3	272	6.18		
P. gracilis	Date	341.2	20	17.06	22.711	**< 0.0001**
	Habitat	1.5	2	0.74	0.379	0.6846
	Habitat x Date	30.2	40	0.76	0.386	0.9997
	Error	529.3	270	1.96		
Combined	Date	625051.4	20	31252.60	16.533	**< 0.0001**
	Habitat	13811.0	2	6905.50	1.918	0.1490
	Habitat x Date	252283.8	40	6307.10	1.751	**0.0053**
	Error	972335.5	270	3601.20		

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CHAPTER 2:

Habitat Use By Nearshore Juvenile And Adult Crab Populations And The Potential Effects Of Predation By Fish And Octopus In Kachemak Bay, Alaska[1]

ABSTRACT

Crab distribution was surveyed in habitats with varying levels of complexity in Kachemak Bay, Alaska. Habitat use was temporally and spatially variable among crab species from June 2005 to September 2006. Nine sites were surveyed monthly using scuba and shrimp pots to quantify crabs and potential crab predators. A total of 388 crabs belonging to four families were observed using scuba surveys and 396 fish and 12 octopuses were caught using shrimp pots. The predominant crab species included *Pugettia gracilis, Oregonia gracilis, Cancer oregonensis,* and *Telmessus cheiragonus*, which made up the majority (97%) of the total crab assemblages. Overall crab abundance increased with habitat complexity; however species richness was not positively correlated with complexity. Predominant species had temporal variation in all habitats. Predatory fish abundance was similar among kelp sites, while octopus abundance was highest at kelp sites with low understory density. Crab abundances may have been influenced by octopus predation; shifts in habitat use may have been driven by temporal variation in understory kelp density. Kelp structure did not have equal importance for all species and varied with species specific crab survival strategy.

[1] Daly B, Konar B (2007) Habitat use by nearshore juvenile and adult crab populations and the potential effects of predation by fish and octopus in a high-latitude region. Prepared for submission in Hydrobiologia

INTRODUCTION

Structural complexity can influence the distribution and abundance of an organism (Underwood and Chapman 1989, Hixon and Menge 1991, Beck 2000, Hovel and Lipcius 2002). Complex three dimensional structure provided by seagrass beds (Attril et al. 2000), mangroves (Ashton et al. 2003), kelp forests (Graham 2004), and coral reefs (Hixon and Beets 1993) can increase biomass, biodiversity, and species richness. Predation, competition, food availability, and larval dynamics co-vary with structural complexity (Lohrer et al. 2000, Almany 2004) resulting in habitat partitioning within an ecosystem. This allows multiple species to co-exist in separate ecological niches (Hines 1982, Downes et al. 1998, Attrill et al. 2000, Almany 2004).

Crabs are an important trophic link in nearshore systems and have significant ecological importance by acting as a food source for many taxa. As omnivores, crabs are key consumers influencing food web dynamics (Polis and Strong 1996, Buck et al. 2003). Crabs rely on habitat complexity for a variety of reasons. Crabs will select particular habitat types and complexities to gain refuge from predation and compete for resources (Hines 1982, Fernandez et al. 1993, Buck et al. 2003). Competition among crabs results in different strategies for habitat use, as required levels of protection are specific for foraging behavior. In areas with macrophytes, spider crab abundance can be influenced primarily by vegetation surface area (Hines 1982). Abundances of *Hemigrapsus sanguineus* and *Leptodius exaratus* can be directly affected by substrate structural complexity (Lohrer et al. 2000). The level of protection acquired from being associated

with certain substrates can influence crab dietary choice and increase survivorship (Hovel and Lipcius 2001, 2002, Buck et al. 2003, Hovel 2003, Lindsey et al. 2006).

Predation pressure co-varies with complexity and influences habitat selection (Holbrook and Schmitt 1988, Heck and Crowder 1990, Richards 1992, Hovel and Lipcius 2002). Different habitat types allow crabs to exploit various spatial refuges and concealment strategies to gain protection from predators (Hines 1982, Hovel and Lipcius 2001). Predator success is often greater in small, patchy environments where edge habitat is proportionately higher (Hovel and Lipcius 2001, 2002). Increased structure enables mobile species to forage independently from predators and allows more available space for prey items (Holbrook and Schmitt 1988, Lohrer et al. 2000). Benthic fish and octopus associated with kelp habitats are known to prey on decapods (Hines 1982, Norton 1991, Tokranov 1995, Vincent et al. 1998, Dodge and Scheel 1999, Kwak et al. 2005). Kelp-associated species such as *Pugettia producta* do not actively search for distant food sources via chemosensory stimuli (Zimmer-Faust and Case 1982). In fact, *P. producta* may rely heavily on habitat structure for nearby food searches and opportunistic feeding strategies.

Kelp beds are extremely productive and diverse ecosystems that provide complex three-dimensional structure (Foster and Schiel 1985). Understory kelps, macroalgae with short stipes and blades extending no more than a few meters above the benthos, provide structure and can inhibit bottom water flow and particle transport (Eckman et al. 1989). Canopy kelps, macroalgae with long stipes and blades that extend to the surface of the water, affect small scale current regimes (Jackson and Winant 1983); however, they

provide little structure in the benthos. In kelp beds, crabs are important trophic links and are preyed on by invertebrates, birds, sea otters, and fish. Kelp structure influences crab density, size variability, and microhabitat resource partitioning (Hines 1982). Macroalgal associated crabs have the highest densities towards the middle of kelp forests (Hines 1982), suggesting they prefer areas with minimal edge effects and maximum structure.

Habitat selection and spatial distribution of specific crab species have been examined in numerous studies (Hines 1982, Feder and Jewett 1986, Fernandez et al. 1993, Moles and Stone 2002, Rooper et al. 2002), but what is lacking is documentation of entire crab community structure in macroalgal habitats. I surveyed nearshore crab abundance and species diversity at specific locations in Kachemak Bay, Alaska with respect to varying macroalgal cover and topographical relief. I hypothesized that (1) overall crab abundance is higher in habitats with high complexity than habitats with low complexity; that (2) species richness is higher in habitats with high complexity than habitats with low complexity; and (3) predator abundance will be negatively correlated with overall crab abundance. Overall complexity can be interpreted as topographical complexity of the substrate, increased macroalgal surface area, or habitat heterogeneity (Beck 2000). I investigated the effects of habitat complexity provided by topographic relief and kelp cover on small spatial scales, and also explored the possibility of predator interactions influencing crab distribution.

MATERIALS AND METHODS

Study area. This study was conducted in Kachemak Bay, located in lower Cook Inlet, Alaska (Fig. 2.1, 59°30'N, 151°30'W). Kachemak Bay hosts a variety of habitats

with substrates of rock, sand, silt, and shell debris (Feder and Jewett 1986). The southern portion of the bay has lush kelp beds with both canopy and understory while the northern bay has a patchy kelp distribution (Feder and Jewett 1986). Nine sites in Kachemak Bay were selected based on structural habitat characteristics (substrate complexity, kelp density). The three canopy sites had a canopy and understory kelp community, the three understory sites contained an understory kelp community, and the remaining three sites were sand. Kelp density has seasonal variability with highest densities in summer and lowest densities in winter (Hamilton and Konar 2007, Daly and Konar 2007). During this study, typical canopy density at canopy sites was 5.29 ± 0.71 stipes $\cdot$ 60 m^{-2} and was dominated by *Nereocystis luetkeana*, while dominant understory species were *Laminaria* spp., *Saccharina* spp., and *Agarum clathratum* (Daly and Konar 2007). Typical understory density at canopy sites was 4.45 ± 0.017 stipes $\cdot$ 0.25 m^{-2}, while understory sites had densities of 3.04 ± 0.122 stipes $\cdot$ 0.25 m^{-2} (Daly and Konar 2007). No canopy and little understory were seen at sand sites. All sites had similar physical oceanographic characteristics (temperature, salinity) and all kelp sites were topographically complex with large boulders and high levels of rugosity (Daly and Konar 2007).

Habitat surveys. Kelp assemblages were measured monthly from June 2005 to September 2006 to document seasonal variation in kelp density using transects and quadrats and scuba techniques (Daly and Konar 2007). Average substrate size and rugosity was measured at each site in May 2005 and September 2006 to quantify substrate complexity (Daly and Konar 2007).

Crab surveys. Benthic scuba surveys were used to quantify temporal and spatial distribution of crabs greater than 5 mm. Three 30 m x 1 m random transects at a depth of approximately 10 m were visually surveyed monthly from June 2005 to September 2006 at each site. In addition, six 0.25 m^2 quadrats were randomly placed along each transect to assess highly cryptic species. All crabs except pagurids were identified to species (Jensen 1995) and counted.

Potential predator surveys. Shrimp pots were deployed from June 2005 to September 2006 at each site to survey potential predators, particularly fish and octopus. Pots were collapsible rectangular 86 cm x 43 cm shrimp traps with a mesh size of 1.25 cm and two 10 cm openings at either end that were funnel shaped and pointed inward. Two pots were randomly placed at each site bi-weekly during the summer of 2005 and monthly thereafter during neap tides. Pots were baited with one frozen herring, and placed at least 5 m apart, and soaked for 48 hours. Organisms caught were identified, counted, and released at the capture location. Octopuses greater than approximately 1 kg were considered crab predators based on previous crab size versus octopus wet weight data (Vincent et al. 1998). Abundances of organisms caught in shrimp pots are listed as catch per unit effort (CPUE).

Statistical analysis. Linear models and multivariate approaches with STATISTICA v.6 (Statsoft, Tulsa, OK, USA) were used for statistical analysis. A repeated measures analysis of variance (ANOVA) and post-hoc comparisons (Tukey's Honestly Significantly Different) were used to determine significance in overall crab abundance, dominant crab abundance, and predators (fish and octopus) among habitats

over time. Correlations between crabs and predators were tested. Significance was determined with an alpha level of 0.05.

RESULTS

Juvenile and adult crabs

A total of 388 crabs belonging to four families were observed in scuba surveys. Most crabs were identified to species. Predominant species included *Pugettia gracilis, Oregonia gracilis, Cancer oregonensis,* and *Telmessus cheiragonus*, which made up the majority (97%) of the total crab assemblages (Table 2.1). Some cancer crabs were unidentifiable to species and were classified as unknown *Cancer*.

Crab distribution was variable in seasonality and habitat use. Crab abundance was maximum in late summer with higher overall numbers at canopy sites (Fig. 2.2). Overall crab abundance varied significantly over time and in habitat use (Repeated measures ANOVA, Table 2.2). The general trend was an increase in crab abundance from low to high habitat complexity (Table 2.1). Canopy sites had significantly more crabs than sand sites (Tukey's HSD, $p < 0.0001$). Understory sites were not significantly different from sand and canopy sites. There was no habitat by time interaction in overall abundances (Table 2.2).

Crab assemblages varied in each habitat suggesting habitat use is species specific. All habitats had similar overall species richness; however each habitat was predominated by few but different species (Fig. 2.3, Table 2.1). *Pugettia gracilis* and *Oregonia gracilis* were the predominant species at understory and canopy sites. *Oregonia gracilis* and *Telmessus cheiragonus* were the predominant species at sand sites. *Pugettia gracilis*

abundance was significantly different over time and by habitat, and had a time x habitat interaction (Table 2.2, Fig. 2.4A). Abundance of *P. gracilis* was significantly higher in canopy sites than understory (Tukey's HSD, $p < 0.0001$) and sand (Tukey's HSD, $p < 0.0001$) sites. *Oregonia gracilis* abundance varied over time and had no habitat effect or time interaction (Table 2.2, Fig. 2.4B). *Cancer oregonensis* abundance did not vary over time, with habitat use, or interactions of the two (Table 2.2, Fig. 2.5A). *Telmessus cheiragonus* varied significantly among habitats but did not vary significantly with time or interaction effects (Table 2.2, Fig. 2.5B). Sand sites had significantly more *T. cheiragonus* individuals than both understory (Tukey's HSD, $p = 0.0033$) and canopy (Tukey's HSD, $p = 0.0033$) sites.

Predators

Shrimp pots caught 396 fish and 12 octopuses. The majority of fish (97%) were hexagrammids, gadids, pleuronectids, and cottids (Fig. 2.6A). Several rare fish (bathymasterids, serrivomerids) were seldom caught and classified as other. Significant variation was found in fish distribution among habitats (ANOVA, $p = 0.0002$). Hexagrammid abundance in canopy (Tukey's HSD, $p < 0.0001$) and understory (Tukey's HSD, $p < 0.0001$) sites was significantly higher than in sand sites with no significant differences between understory and canopy sites (Tukey's HSD, $p = 0.705$). Cottid (ANOVA, $p = 0.521$) and gadid (ANOVA, $p = 0.872$) abundance was similar among all habitats. All pleuronectids were caught in sand sites. Overall, fish families did not exhibit significant seasonality (ANOVA, $p = 0.397$). Crab abundance did not vary significantly with fish abundance (Fig. 2.7A, $p = 0.805$). *Octopus dofleini* was the only octopus

species caught; all were greater than approximately 2.5 kg. Of the 12 *O. dofleini* caught, 11 were at understory sites (Fig. 2.6B). Octopus distribution varied significantly by habitat (ANOVA, $p < 0.0001$). Understory sites had significantly more octopuses than sand (Tukey's HSD, $p = 0.0005$) and canopy sites (Tukey's HSD, $p = 0.00232$), however there was not a significant crab x octopus correlation (Fig. 2.7B, $p = 0.124$). Octopus were caught throughout the year with no significant seasonality (ANOVA, $p = 0.152$).

DISCUSSION

Habitat structural complexity influences species abundance and diversity. In this study, crab abundance varied among habitats with a gradient of overall crab abundances increasing with structural complexity. These data agree with other studies involving habitat complexity and species abundance. As an example, increases in overall invertebrate abundance can correspond to increasing habitat complexity in freshwater macrophyte stands (McAbendroth et al. 2005). Also, crustacean abundance can be highest in areas of high macrophyte biomass and habitat surface area (Stoner and Lewis 1985). In this study, highest crab abundances were found at canopy sites. Interestingly, canopy sites also had the highest density of understory kelp (Daly and Konar 2007). Canopy kelp has the ability to dampen ambient current velocities and can buffer physical factors in kelp habitats (Jackson and Winant 1983, Jackson 1984, 1986, Eckman et al. 1989, 2003, Duggins et al. 1990), however understory kelp probably more directly affects crab ecology than canopy. Most canopy kelp structure is in the water column and not directly available as a crab refuge. The overall trend of increased crab abundance in highly complex habitats was primarily caused by variation in abundance of two species:

Pugettia gracilis and *Oregonia gracilis*. Because few species are causing these fundamental trends, it is important to address effects of habitat complexity on an individual species level.

Species richness did not increase with habitat complexity. Other researchers studying effects of habitat complexity on species richness and diversity have had mixed results (Johnson et al. 2003, Tanaka and Leite 2003, McAbendroth et al. 2005). Seagrass structural complexity does not directly influence the composition of associated macroinvertebrates (Attrill et al. 2000), but opinions vary (Bologna and Heck 2002, Taniguchi and Tokeshi 2004). Species richness, diversity, and abundance were positively correlated with increased seagrass biomass and highly complex substrate in freshwater streams (Bologna and Heck 2002, Taniguchi and Tokeshi 2004). In this study, species composition varied among habitats, however species richness was similar regardless of complexity.

Crab assemblages were dominated by few species, suggesting that each species occupies a specific ecological niche. For example, *Pugettia gracilis* was found primarily on the tops of understory macroalgae, while *Cancer oregonensis* occupied empty barnacle tests (Jensen 1995, Daly, personal observation). Distributions of these species may be regulated by available habitat for the survival strategy of each crab species. Increased understory is likely to increase densities of species directly affected by the structure that it provides. Conversely, decreased understory density may provide more available space on the substrate for barnacles to settle providing a more suitable habitat for *C. oregonensis*.

Oregonia gracilis has the most complex decoration of all northern decorator crabs (Jensen 1995) and covers itself with pieces of its surroundings. This species is usually found directly on the substrate (Daly, personal observation) and may be less affected by kelp structure than other species. As such, *O. gracilis* was observed in similar numbers in all habitats. Because this species actively uses small pieces of biogenic debris to decorate itself, three dimensional kelp structure may be less critical for avoiding predators. Drift kelp was observed at all sites, including sand sites. Drift kelp availability may directly influence *O. gracilis* distribution.

Telmessus cheiragonus was most commonly seen in sand sites and is known to bury itself to avoid predation (Jensen 1995). Soft sediment is required for this behavior, which is an important component for this species life history. Because kelp beds are found in areas with hard substrate, *T. cheiragonus* habitat preference may be influenced by substrate and not kelp structure.

Temporal variability in habitat use may be determined by seasonal behavior and migrations on various spatial scales. For example, *Pugettia gracilis* was most abundant in late summer with numbers decreasing throughout the winter. Little is known about the migration patterns of this species. *Pugettia* spp. may undergo spatial migrations (Wicksten and Bostick 1983), although Hines (1982) could find no seasonal movement of tagged crabs in Monterey Bay, California. However, seasonal effects may be more pronounced at higher latitudes where variations in temperature, salinity, and light/dark regimes can be more intense. *Pugettia gracilis* migrations most likely occur at small spatial scales. If this species had a large scale spatial migration in winter, no crabs would

be expected once the environmental threshold was reached. However, *P. gracilis* was observed in low densities in winter suggesting temporal variability of this species was a function of changes in habitat use, not large scale migrations by all individuals. *Pugettia* spp. eat kelp almost exclusively (Hines 1982) so moving to deeper waters with less food would not be beneficial. However, some crab species can go long periods (>6 months) without eating (Schultz and Shirley 1997). Perhaps *P. gracilis* utilizes rock substrate for protection in winter when kelp densities are lowest. Inhabiting substrate cracks and crevices would make them less visible to divers, resulting in lower observed winter numbers.

Other species also had temporal variation in habitat use. *Telmessus cheiragonus* was not observed during winter in any habitat. *Telmessus cheiragonus* bury themselves in sediment for long periods (Jensen 1995), which may occur in winter to conserve metabolic demands and avoid predation. Warmer spring temperatures may trigger this species to become active and begin foraging for food. *Telmessus cheiragonus* may migrate to deeper water in winter; however, *Telmessus* spp. eat bivalves and other infauna (Oikawa et al. 2002), which occur in many habitats. *Cancer oregonensis* had peak abundances in both summer and winter. Because this species was associated with high substrate complexity and empty barnacle tests, kelp structure is likely to have less effect on its distribution. *Oregonia gracilis* is also less likely to be directly affected by kelp structure. This species relies heavily on decoration and substrate complexity to conceal itself from predators. However, *O. gracilis* numbers also decreased in winter. With colder temperatures, crabs are expected to be less active as metabolic rates are

lower (Leffler 1972, DeWachter and McMahon 1996). Because *O. gracilis* is highly cryptic and camouflages itself effectively, reduced mobility makes detection of individuals more difficult. As such, fewer would be seen by divers.

Predation pressure may influence crab abundance. Benthic fish associated with kelp habitats are known to feed primarily on decapods (Norton 1991, Tokranov 1995, Kwak et al. 2005). Although many gadids are pelagic, they also are known to feed on decapods (DuBuit 1989, Morte et al. 2001). In this study, cottids, hexagrammids, and gadids had similar densities in all kelp sites. As such, differences in crab densities between understory and canopy sites were probably not influenced by fish predation. Pleuronectids were only caught in sand sites and may reduce crab abundances, however the majority of crabs observed (*Pugettia gracilis* and *Oregonia gracilis*) are kelp associated and were not expected to have high densities in these areas. Because fish abundances were similar in kelp sites, differences in crab distribution may not have been determined by fish predation. However, large *Hippoglossus stenolepis* (Pacific halibut) may have been present and would not be effectively surveyed via shrimp pots. *Enhydra lutris* (sea otter) were not surveyed and may have influenced crab abundance.

Octopus dofleini had highest densities in understory sites. *Octopus dofleini* prefer boulder areas with dense understory kelp (Scheel 2002), as reported in this study. Prey availability may influence *O. dofleini* habitat selection (Scheel 2002). Field studies have shown *O. dofleini* inhabit areas with high relative crab densities and are generalists feeding on a variety of crab species (Vincent et al. 1998). In Alaska, midden piles found outside occupied octopus dens have revealed *Pugettia gracilis, Cancer oregonensis,*

Telmessus cheiragonus, Oregonia gracilis, Hyas lyratus, and *Phyllolithodes papillosus* to be prey (Vincent et al. 1998, Dodge and Scheel 1999). Seventy percent of an intertidal octopus diet consisted of crabs, and they consumed an average of 3.1 hard bodied prey items per day (Vincent et al. 1998). Similar consumption rates could be expected for subtidal octopus. Also, octopuses stay in a single area for several weeks (Vincent et al. 1998), suggesting foraging behavior within a home range. At three crabs per day, one resident octopus has the potential to significantly affect a local crab community. Perhaps the increase in octopus predation at understory sites in this study decreased *P. gracilis* densities. Anecdotal observations of *C. oregonensis* and *P. gracilis* remains in pots with octopuses confirm the octopuses were feeding on crabs. Differences between crab abundances or assemblages may have resulted from octopus predation. Furthermore, lower understory densities at understory sites would leave crabs more vulnerable to octopus predation. However, these data simply indicate that crab and octopus densities vary by habitat. Crabs and octopus may rely on different habitats and may not be directly influencing each other.

Sampling bias may influence temporal and spatial variability of crab observations and shrimp pot efficiency. Scuba surveys can underestimate benthic organism densities (Coyer et al. 1999). In complex habitats, crabs become increasingly difficult to observe. However in this study, crab densities were highest at the most complex sites. More crabs would be expected to be observed with lower kelp densities. Therefore, crab abundances in complex sites are conservative. Scuba surveys are inherently biased for certain species. For example, *Fabia subquadrata* live inside live mussel shells as juvenile and adults,

while *Rhinolithodes wosnessenskii* reside in rock crevices (Jensen 1995). Dive surveys are thus not effective for quantifying these species. As a result, species diversity and richness may be underestimated. The size of the shrimp pots limit the number and size of organisms caught. Bait also influences trap efficiency and may be species selective. Shrimp pots do not indicate absolute fish and octopus abundances; however relative comparisons between sites can be made. Anecdotal visual surveys confirm shrimp pot data in terms of relative fish composition and octopus abundance.

Species have different behaviors to evade predation and compete for resources. Importance of substrate complexity and kelp structure is unique depending on survival strategy and behavior. Because canopy kelps provide little structure in the benthos, they are thought to have little importance to juvenile and adult crabs. Understory had highest densities in canopy sites and probably influenced *Pugettia gracilis* abundance, while *Oregonia gracilis* may depend on kelp for decoration, rather than protection provided by structure. *Cancer oregonensis* and *Telmessus cheiragonus* habitat use suggests substrate complexity is more important than kelp structure for survival of these species. Predation may have affected the variability of crab abundance among sites. Fish abundance was similar in all kelp sites suggesting similar fish predation. Octopus densities were highest in understory sites and may have reduced crab abundance. The synergistic relationship of habitat complexity and predation is a fundamental concept influencing habitat use and distribution of nearshore crabs.

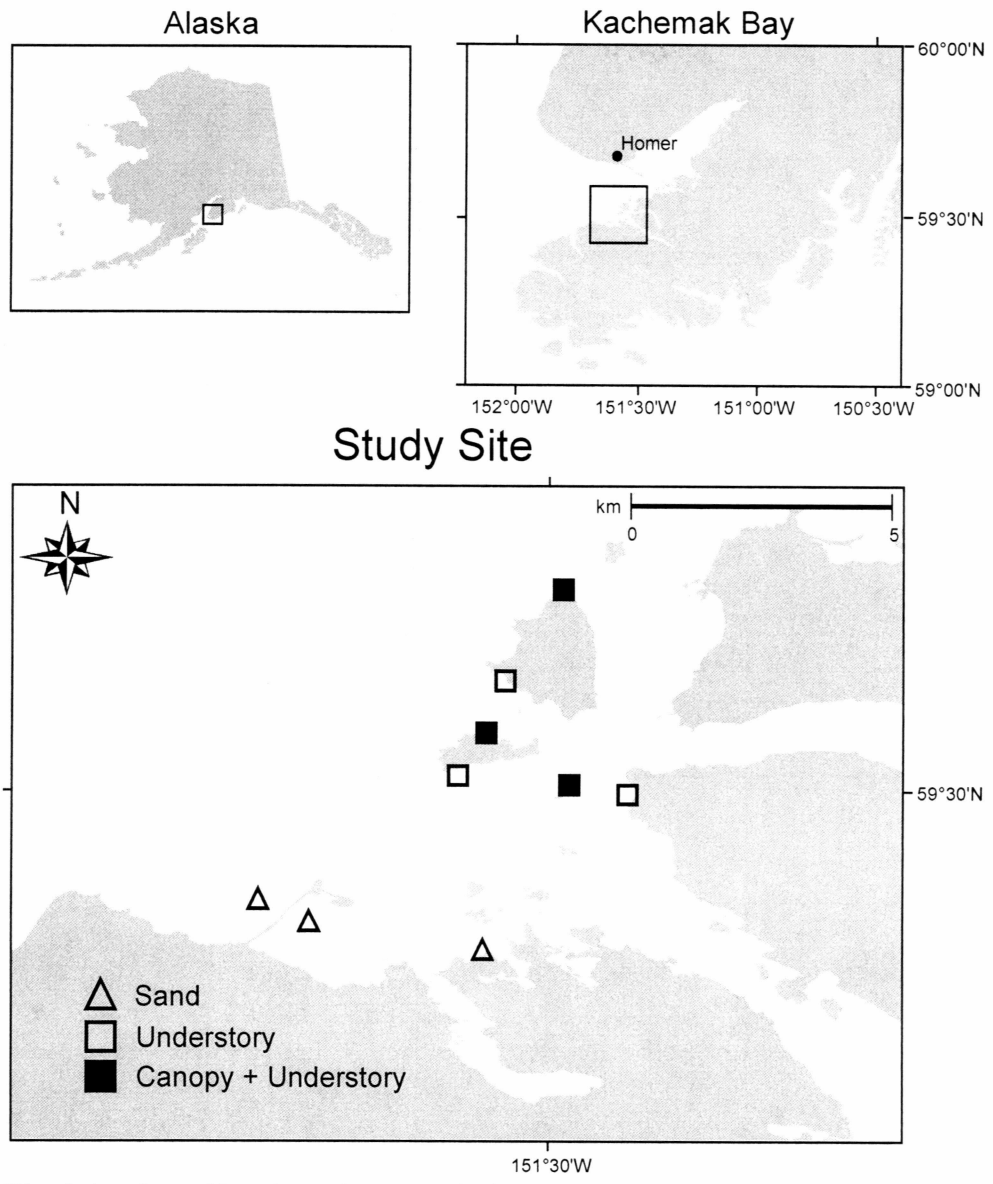

Fig. 2.1. Map of Kachemak Bay, Alaska showing site locations.

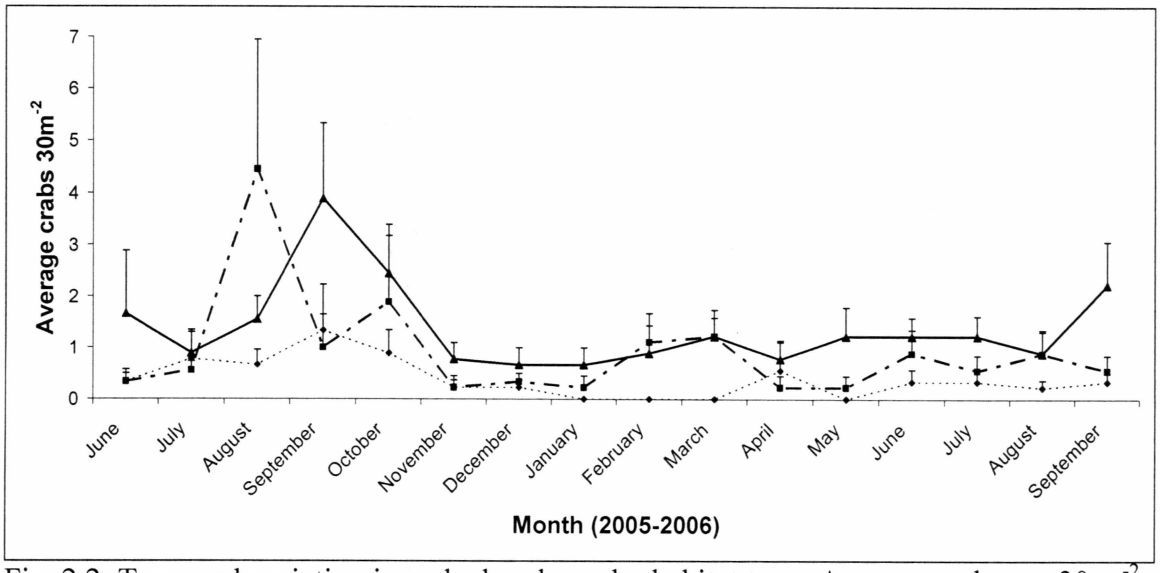

Fig. 2.2. Temporal variation in crab abundance by habitat type. Average crabs per 30 m^{-2} transect. Values are all species combined. Solid lines indicate canopy and understory habitat, dashed lines indicate understory only habitat, dotted lines indicate sand habitat. Error bars are + 1 standard error.

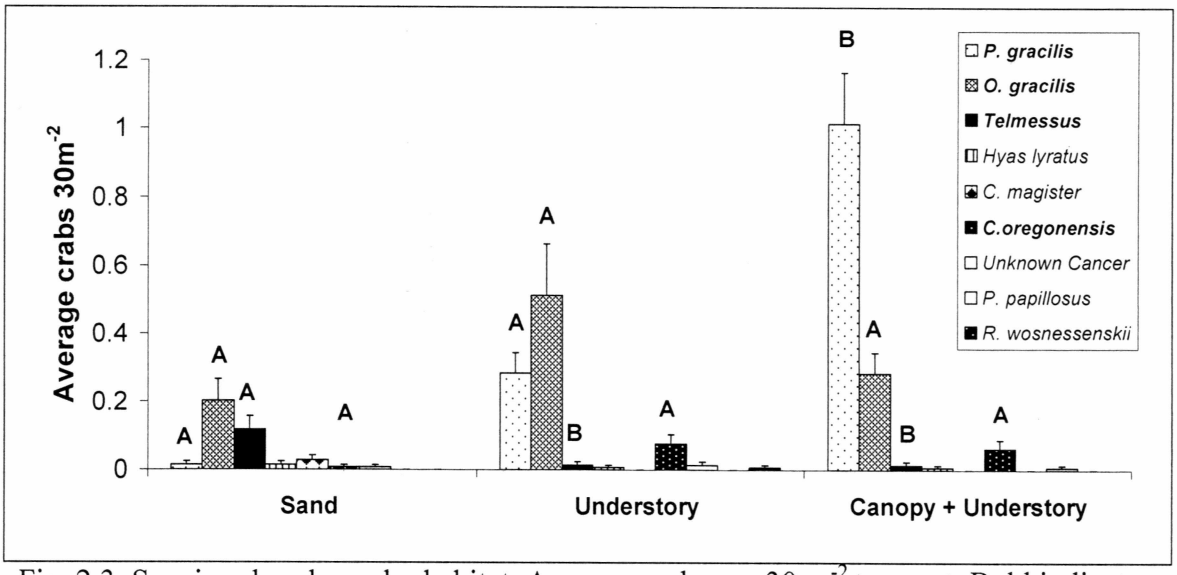

Fig. 2.3. Species abundance by habitat. Average crabs per 30 m^{-2} transect. Bold indicates predominant species. Different letters are significantly different between habitats for individual species. Error bars are + 1 standard error.

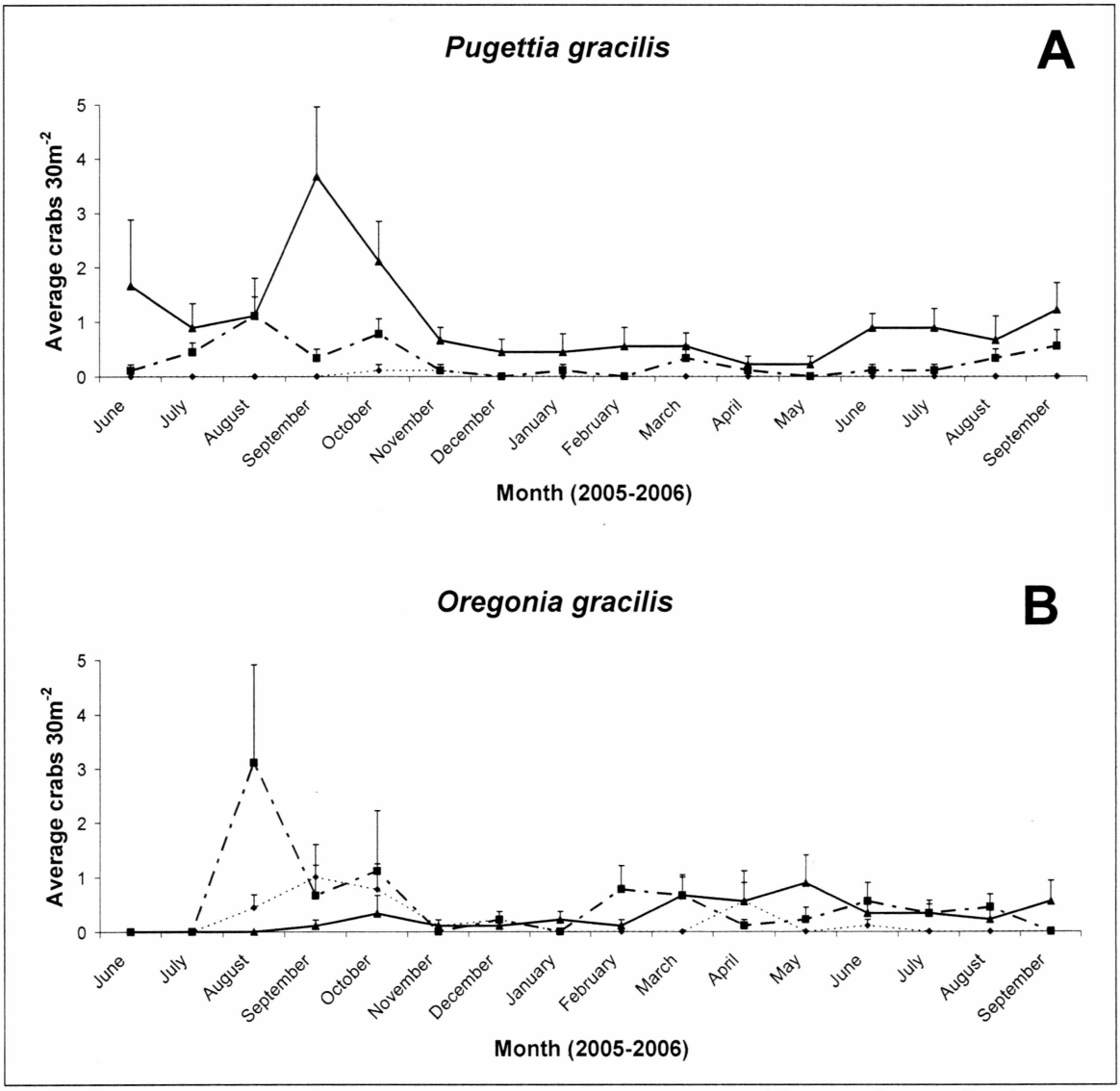

Fig. 2.4. *Pugettia gracilis* (A) and *Oregonia gracilis* (B). Habitat use by predominant species (crabs $30m^{-2}$). Solid lines indicate canopy and understory habitat; dashed lines indicate understory only habitat; dotted lines indicate sand habitat. Vertical bars are + 1 standard error.

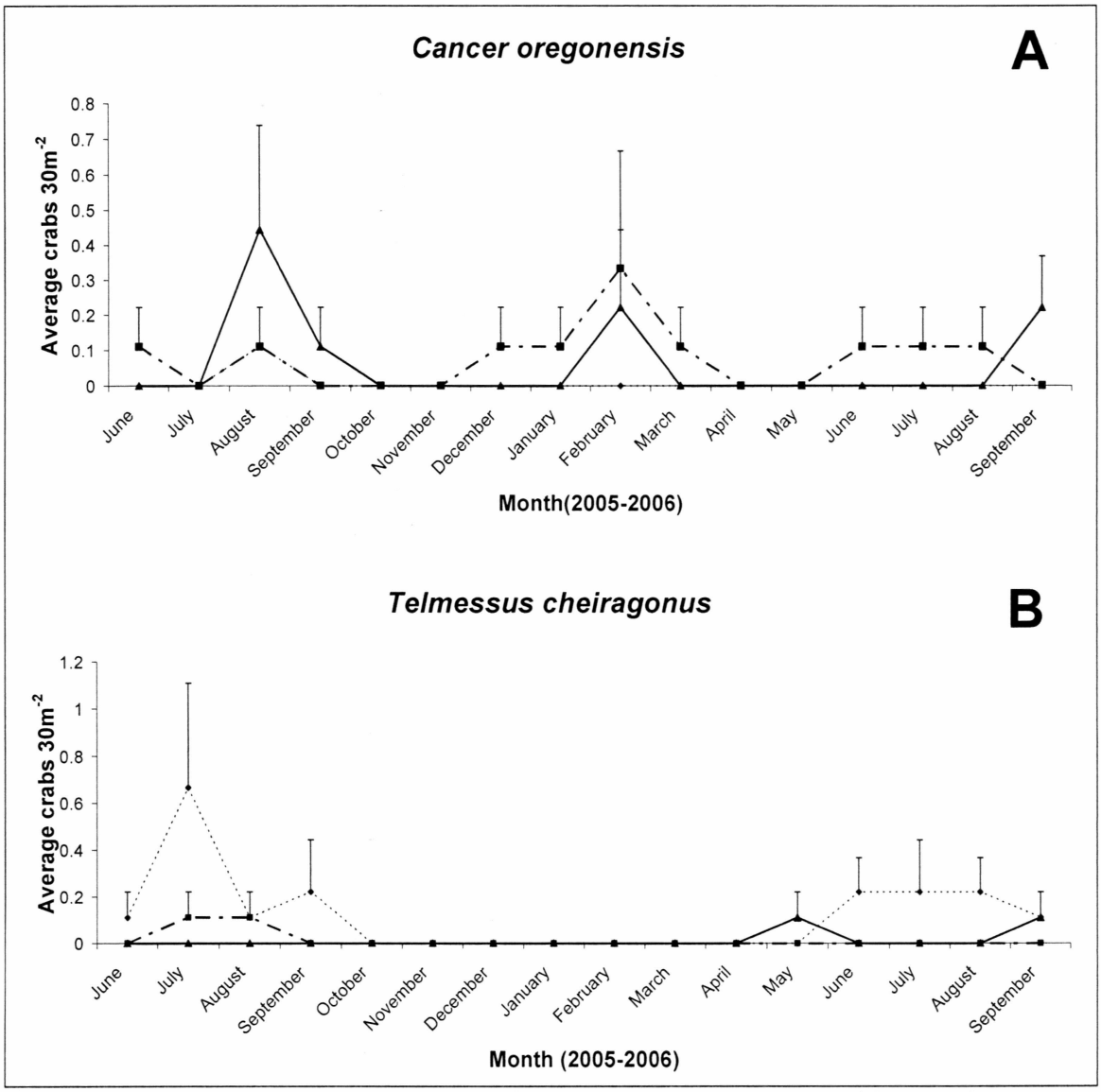

Fig. 2.5. *Cancer oregonensis* (A) and *Telmessus cheiragonus* (B). Habitat use by predominant species (crabs $30m^{-2}$). Solid lines indicate canopy and understory habitat; dashed lines indicate understory only habitat; dotted lines indicate sand habitat. Vertical bars are + 1 standard error.

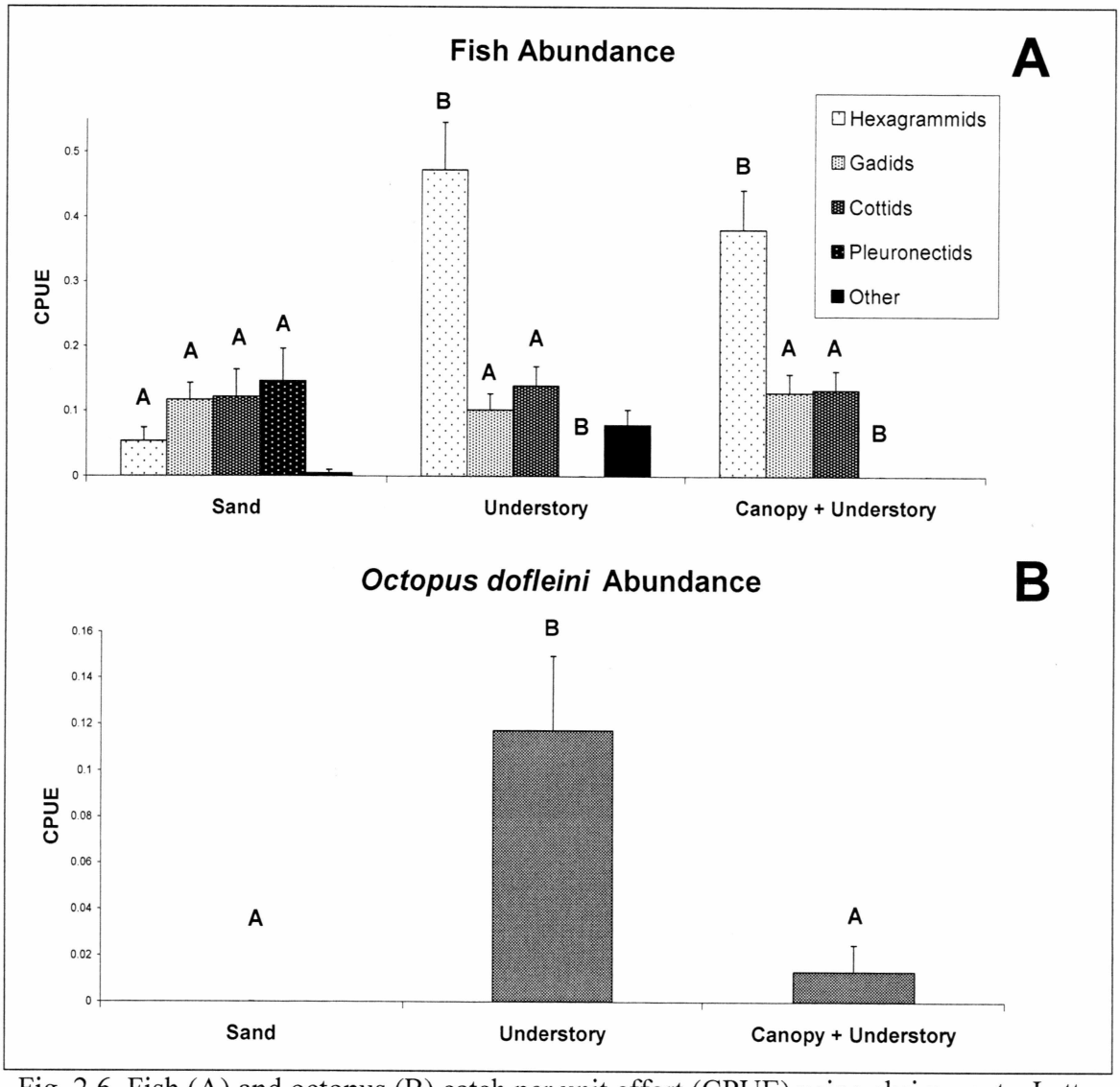

Fig. 2.6. Fish (A) and octopus (B) catch per unit effort (CPUE) using shrimp pots. Letters indicate significant difference between habitats. Error bars are + 1 standard error.

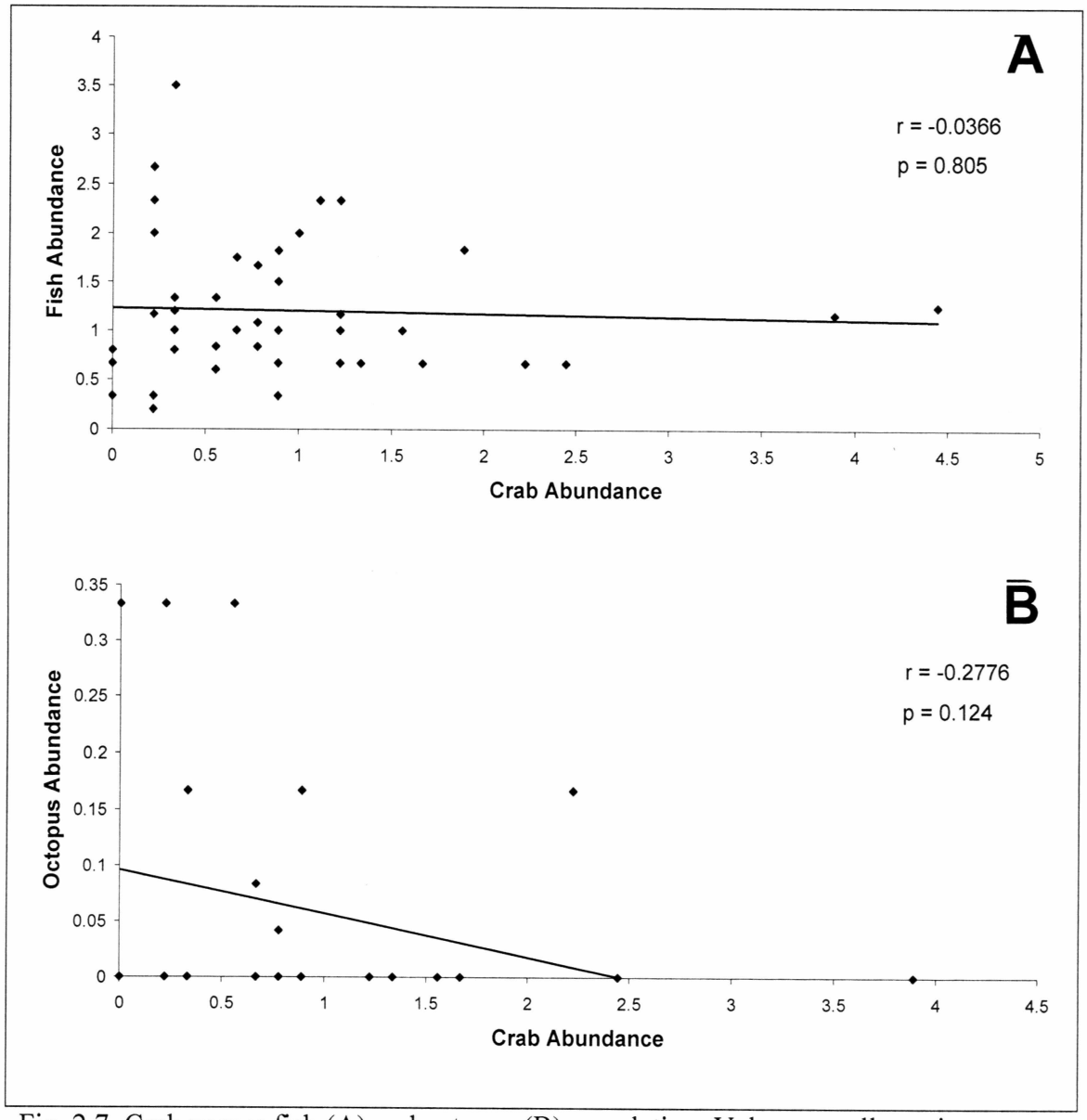

Fig. 2.7. Crab versus fish (A) and octopus (B) correlation. Values are all species combined in all habitats.

Table 2.1. Crab species observed using scuba surveys. Bold indicates the predominant species.

Family, *species name*, common name	**Sand**	**Under**	**Canopy**	**Total**
Majidae				
Pugettia gracilis (graceful kelp crab)	2	41	146	**189**
Oregonia gracilis (graceful decorator crab)	29	74	41	**144**
Hyas lyratus (Pacific lyre crab)	2	1	1	4
Cancridae				
Cancer oregonensis (pygmy rock crab)	1	11	9	**21**
Cancer magister (Dungeness crab)	4	0	0	4
Unknown	1	2	0	3
Cheiragonidae				
Telmessus cheiragonus (helmet crab)	17	2	2	**21**
Lithodidae				
Rhinolithodes wosnessenskii (rhinoceros crab)	0	1	0	1
Phyllolithodes papillosus (heart crab)	0	0	1	1
Total Observed	**56**	**132**	**200**	**388**

Table 2.2. Repeated measures ANOVA results for predominant species of juvenile and adult crabs. Bold indicates statistical significance (α less than or = 0.05).

species	**Source**	**SS**	**df**	**MS**	**F**	**p**
	Date	141.074	15	9.4049	3.2792	**0.0001**
	Habitat	72.074	2	36.0370	9.2501	**0.0001**
Combined	Habitat x Date	123.926	30	4.1309	1.0603	0.3868
	Error	997.333	256	3.8958		
	Date	48.090	15	3.2060	3.2684	**0.0001**
P. gracilis	Habitat	77.042	2	38.5208	32.3912	**< 0.0001**
	Habitat x Date	67.181	30	2.2394	1.8830	**0.0049**
	Error	304.444	256	1.1892		
	Date	37.926	15	2.5284	2.1281	**0.0123**
O. gracilis	Habitat	7.542	2	3.7708	2.5603	0.0793
	Habitat x Date	65.421	30	2.1807	1.4807	0.0569
	Error	377.037	256	1.4728		
	Date	1.683	15	0.1122	1.7310	0.0526
C. oregonensis	Habitat	0.389	2	0.1944	2.4981	0.0842
	Habitat x Date	1.685	30	0.0562	0.7217	0.8576
	Error	19.926	256	0.0778		
	Date	1.757	15	0.1171	1.2974	0.2130
T. cheiragonus	Habitat	1.042	2	0.5208	7.0588	**0.0010**
	Habitat x Date	2.736	30	0.0912	1.2361	0.1926
	Error	18.889	256	0.0738		

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GENERAL CONCLUSIONS

This study demonstrated the importance of documenting temporal and spatial variability in crab distribution. Temporal documentation of specific crab larvae in Kachemak Bay is useful for future researchers who want to study a single species. Also, documentation of habitat use in terms of architectural complexity is helpful when understanding how specific habitat characteristics may affect juvenile and adult crab distribution. Some species appeared in Kachemak Bay in certain life stages exclusively. Management efforts must consider temporal and spatial variation in each life history stage and the ecological importance of each crab species when making generalizations about a habitat.

Larval timing and the importance of habitat structural complexity for spatial distribution of juvenile and adult crabs is species specific and varies with survival strategy. The dramatic seasonality of environmental variables (tides, temperature, salinity, light, phytoplankton blooms) may regulate the timing of larval hatching. Spatial differences in larval abundance probably resulted from large scale physical transport mechanisms. This study suggested that *Nereocystis luetkeana* canopy structure had minimal effects on spatial crab distribution in all life stages. In fact, *Nereocystis luetkeana* may have little importance to juvenile and adult crabs. Understory may more directly affect crabs by providing more structural refuge. For juvenile and adult crabs, the importance of substrate complexity and kelp structure is species specific and may be influenced by predation pressure. Habitat use and the importance of structural complexity vary by life history stage and species depending on survival strategy.

Future studies on larval dynamics and recruitment in kelp beds may prove useful in understanding adult population distributions in these habitats. A flow rate comparison between inner and outer canopy kelp habitats might aid in understanding the effects of kelp structure on local hydrodynamics. Standardizing structure via artificial kelp would further elucidate kelp effects on flow regimes. Focusing on a single crab species using a short, concentrated sampling effort may be helpful to understand small scale temporal variation and kelp structure effects on spatial larval crab distribution.